

REVIEW ARTICLE

Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology

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Abstract

Apes, members of the superfamily Hominoidea, possess a distinctive suite of anatomical and behavioral characters which appear to have evolved relatively late and relatively independently. The timing of paleontological events, extant cercopithecine and hominoid ecomorphology and other evidence suggests that many distinctive ape features evolved to facilitate harvesting ripe fruits among compliant terminal branches in tree edges. Precarious, unpredictably oriented, compliant supports in the canopy periphery require apes to maneuver using suspensory and non-stereotypical postures (i.e. postures with eccentric limb orientations or extreme joint excursions). Diet differences among extant species, extant species numbers and evidence of cercopithecoid diversification and expansion, in concert with a reciprocal decrease in hominoid species, suggest intense competition between monkeys and apes over the last 20 Ma. It may be that larger body masses allow great apes to succeed in contest competitions for highly desired food items, while the ability of monkeys to digest antifeedant-rich unripe fruits allows them to win scramble competitions. Evolutionary trends in morphology and inferred ecology suggest that as monkeys evolved to harvest fruit ever earlier in the fruiting cycle they broadened their niche to encompass first more fibrous, tannin- and toxin-rich unripe fruits and later, for some lineages, mature leaves. Early depletion of unripe fruit in the central core of the tree canopy by monkeys leaves a hollow sphere of ripening fruits, displacing antifeedant-intolerant, later-arriving apes to small-diameter, compliant terminal branches. Hylobatids, orangutans, *Pan* species, gorillas and the New World atelines may have each evolved suspensory behavior independently in response to local competition from an expanding population of monkeys. Genetic evidence of rapid evolution among chimpanzees suggests that adaptations to suspensory behavior, vertical climbing, knuckle-walking, consumption of terrestrial piths and intercommunity violence had not yet evolved or were still being refined when panins (chimpanzees and bonobos) and hominins diverged.

Key words: arm-hanging; Cercopithecoidea; Hominoidea; Miocene; suspensory behavior; vertical climbing.

Introduction

Humans diverged from panins approximately 6–7 million years ago, yet for several million years after the split, up until the appearance of *Homo*, hominins continued to share numerous traits with chimpanzees and bonobos, including body mass (McHenry & Berger, 1998), cranial capacity (and presumably therefore many aspects of cognition; Schoenemann, 2006), and much of their thoracic and forelimb anatomy (Senut, 1978; Tardieu, 1981; Stern & Susman, 1983). In other words, for much of human evolution early

hominins remained in essence bipedal chimpanzees. However, not all paleontologists view traits shared by australopiths and chimpanzees as particularly informative; through the early 1960s and even later some scholars considered australopiths to be quite human-like, a perspective that interprets ape-like traits as primitive retentions. In the 1980s this perception began to shift (Stern & Susman, 1983; Cartmill et al. 1986; Cartmill & Smith, 2009). Accumulating data on the behavior of wild chimpanzees revealed a surprisingly human-like inventory of behaviors (Goodall, 1968, 1986), nudging the perception of chimpanzee nature closer to that of humans and causing some scholars to reconsider decades old evidence of cognitive sophistication among the apes (Kohler, 1925/1959; Kohts, 1935/2002). As the scope of not only behavioral similarities but biochemical similarity (Goodman et al. 1987) became clear, and in accord with evidence that chimpanzees and bonobos are more closely related to humans than to gorillas (Mikkelsen et al. 2005;

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Accepted for publication 15 January 2016

Article published online xx xx xx

Prüfer et al. 2012), some scholars even advocated placing chimpanzees in the genus *Homo* (Wildman et al. 2003). Among the shared characters currently viewed as linking humans and panins are: a fission-fusion social system (Goodall, 1968; Nishida, 1968; Wrangham, 1979), a capacity for coalitionary violence (Wrangham, 1999), manufacture and use of tools (Goodall, 1964; Boesch & Boesch, 1983; McGrew, 1992), mental mapping ability (Boesch & Boesch, 1984; Mendes & Call, 2014), numeracy (Matsuzawa, 1985; Rumbaugh et al. 1987), spatial memory (Tinklepaugh, 1932; Menzel, 1973), political ideation (de Waal, 1982; Nishida, 1983), self-concept (Tomasello et al. 2005; Hare et al. 2000; Wobber et al. 2014), digestive physiology (Lambert, 2002; Perry et al. 2007), dependence on hunting and meat eating (Wrangham, 1977; Boesch & Boesch, 1989; Wrangham & Bergmann-Riss, 1990), life history (Schultz, 1940; Gavan, 1953; Ulijaszek, 2002; Smith et al. 2013), language comprehension (Gardner & Gardner, 1969; Savage-Rumbaugh et al. 1985), gestural and whole-body communication (Woodruff & Premack, 1979; Goodall, 1986), capacity for culture (Wrangham et al. 1994; Whiten et al. 1999), neuroanatomy (Gannon et al. 1998; Semendeferi et al. 2001), and perhaps capacity for empathy (de Waal, 2008). Each of these traits grew out of ecological adaptations that evolved in the shared human/panin ancestor during the MioPliocene, and explaining their evolution is bound up in the question of why apes exist. Humanness is, to an unexpectedly great extent, apeness. Tracing the evolution of ape and monkey ecomorphology is therefore a particularly compelling area of study for human paleontologists because without an understanding of why there are apes we cannot begin to understand why there are humans.

Perhaps unexpectedly, when we turn to anatomy there is less resemblance; instead, chimpanzees and bonobos more closely resemble the other great apes, gorillas and orangutans, more than humans. Many great ape specializations are thought to have evolved as adaptations to suspensory behavior, vertical climbing or both. The ubiquity of these anatomical synapomorphies is somewhat mysterious because these traits did not appear in apes at the time of their divergence from monkeys, perhaps 25 million years ago, but much later. Even more bewildering, there is growing evidence that many derived features shared by the apes not only evolved late, they evolved in parallel in each of the various lineages, rather than in a shared common ancestor. Wrangham (1980), Andrews (1981), Temerin & Cant (1983) and others have offered compelling evidence that this homoplastic phenomenon grew out of competition between Old World monkeys and apes (but see Harrison, 2010b for a thoughtful counterpoint).

An attempt to sort out the competitive and co-evolutionary relationship among apes and monkeys might seem premature, yet the time for such a synthesis never seems right. Forty-five years ago, Napier (1970) wondered whether it might be rash to attempt the task then, given that it

required interpreting an incomplete fossil record while simultaneously synthesizing data from a diverse assortment of scientific disciplines, some of which were new and rapidly expanding (Napier, 1970). Now a half century later the situation has scarcely improved. While the fossil record is more complete, there is little agreement as to which of the various late Miocene apes is the common ancestor of African apes and humans. Still, there is enough of a signal among the noise that a number of scholars have tackled the ape-origins problem (Ripley, 1979; Wrangham, 1979, 1980; Andrews, 1981; Temerin & Cant, 1983; Harrison, 1987; Rose, 1993; Pilbeam, 1996; Larson, 1998; Crompton et al. 2008; Fleagle, 2013). This review will draw on these syntheses extensively as the current understanding of extant ape and monkey functional anatomy, socioecology, evolutionary history, and the interrelationships among these disciplines are reviewed. This review will be limited largely to features that have functional consequences, such as limb-segment length, muscle size, joint morphology and dental morphology, ignoring features such as arterial branching and relative surface areas of individual cranial bones that – while helpful for resolving evolutionary relationships – are probably consequences of drift (Cheverud, 1982). Particular attention will be paid to morphology that both informs ecological niche adaptations and can be linked most confidently to positional (i.e. locomotor and/or postural) behavior, although at times physiology and genetics will also be considered. Discussion will be limited to primates while acknowledging that other species, such as bats, birds, squirrels, insects, fungi and bacteria, are certainly important competitors to both monkeys and apes. It is reasoned that the similarities in digestive physiology, cognition, food-perceiving senses, body size and morphology strongly influence access to food resources, and make it likely that monkeys and apes are one another's most important competitors. Regarding this issue, David Lack argued that comparisons among closely related taxa are most trenchant because 'the more similar the compared taxa are in all other respects, the more chance the biologist has to detect the reason for any differences that exist' (Harcourt & Stewart, 2007, p. 11). In keeping with this philosophy, this review will focus on competition between chimpanzees and sympatric African monkeys, in part because African primates were sympatric with hominins humans throughout their evolutionary history, in part because African apes are phylogenetically closest to the human lineage and also, not insignificantly, because the author is most familiar with African primates.

Extant cercopithecoid ecomorphology and socioecology

Although the Cercopithecoidea has adapted to diverse habitats with diverse adaptations, the 136 species of extant cercopithecoids (Old World monkeys; largely following the

Fleagle, 2013 taxonomy; also Groves, 2001; Table 1) can be parsed into three ecomorphological groups that, unavoidably, sometimes cross taxonomic lines: the colobines; the arboreal cercopithecines; and the terrestrial cercopithecines. This 'unnatural' (i.e. paraphyletic) grouping is argued to be best inform discussions of competition, adaptation and niche-packing, rather than strictly adhering to phylogenetic relationships.

Colobines

The 61 species of colobines monkeys (subfamily Colobinae) range widely across Africa and Asia. They weigh 4–15 kg (female mass; after Smith & Jungers, 1997; Fleagle, 2013), more than the arboreal cercopithecines. They are sexually

dimorphic compared to most primates; females are on average 77% of the body weight of males (Table 2). This degree of sexual dimorphism is widely regarded as having evolved due to the advantage large body size, large canines (Kay et al. 1988; Plavcan & Van Schaik, 1992), large gapes and powerful jaw muscles (Harvey & Harcourt, 1984; Clutton-Brock, 1985; Hylander, 2013) provide in one-on-one male contest competition for reproductive access to females (Plavcan & Van Schaik, 1997).

Colobines live in multifemale groups that often but not always include only a single male (Davies & Oates, 1995; Sterck, 2012). They are female-bonded (Wrangham, 1980; Sterck et al. 1997), with the exceptions of the red colobus and Thomas's langur. They occupy most of the same geographic areas as the cercopithecines and are often seen in

Table 1 Ape and Old World monkey species counts, body masses.

Superfamily	Family	Subfamily	Tribe	Genus	Species count	Common name of exemplar	Male body mass (kg)	Female body mass (kg)			
Cercopithecoidea		Cercopithicinae	Cercopithecini	<i>Allenopithecus</i>	1	Allen's Swamp Monkey	5.9	3.6			
				<i>Miopithecus</i>	2	Talapoin	1.4	1.2			
			<i>Chlorocebus</i>	6	Vervet	5.6	2.8				
			<i>Cercopithecus</i>	26	Guenon	4.8	3.1				
			<i>Erythrocebus</i>	1	Patas Monkey	10.3	5.8				
			Papionini	<i>Macaca</i>	20	Macaque	10.1	6.6			
				<i>Lophocebus</i>	3	Papionan Mangabey	8.3	6.0			
				<i>Papio</i>	6	Savanna Baboon	23.4	12.5			
				<i>Theropithecus</i>	1	Gelada Baboon	26.1	14.0			
				<i>Cercocebus</i>	7	Mandrillan Mangabey	10.0	5.7			
		<i>Mandrillus</i>		2	Mandrill	25.3	8.9				
		Colobinae		<i>Colobus</i>	5	Black and White Colobus	9.6	7.5			
				<i>Piliocolobus</i>	10	Red Colobus	8.4	7.0			
			<i>Procolobus</i>	1	Olive Colobus	4.6	4.2				
			<i>Semnopithecus</i>	7	Gray Langur	18.4	12.0				
			<i>Trachypithecus</i>	18	Leaf Monkey	8.8	7.6				
			<i>Presbytis</i>	11	Surili Langur	6.2	6.3				
			<i>Pygathrix</i>	3	Douc Langur	11.0	8.4				
			<i>Rhinopithecus</i>	4	Snub-nosed Langur	19.3	12.5				
			<i>Nasalis</i>	1	Proboscis Monkey	19.8	9.6				
		<i>Simias</i>	1	Pig-tailed Langur	9.1	6.9					
		Hominoidea	Hylobatidae			<i>Hylobates</i>	13	Gibbon	6.2	6.1	
						<i>Symphalangus</i>	1	Siamang	11.9	10.7	
			Hominidae			Ponginae	<i>Pongo</i>	2	Orangutan	78.2	35.7
						Gorillinae	<i>Gorilla</i>	2	Gorilla	168.5	83.3
Homininae	Panini					<i>Pan</i>	2	Chimpanzee	48.4	39.3	

Table 2 Socioecology and ecomorphology of extant monkeys and apes: implications for fossil primates.

Species	Social system	Body mass (kg) M/F	Mass dimorphism	Canine dimorphism	Canopy use	IMI
Colobines	Multi- or uni-male F-B	10.2/7.9	0.77	Strong ¹	Arboreal	81.4
Arboreal cercopiths	Unimale F-B	7.4/4.7	0.58	Strong ¹	Arboreal	88.8
Terrestrial cercopiths	Multimale F-B	22.8/11.2	0.49	Extreme ¹	Terrestrial	95.9
<i>Papio anubis</i>	Multimale F-B	27.8/13.1	0.47	Extreme ¹	Terr/Arb	97.0
<i>Papio hamadryas</i>	Female-choice	19.1/10.9	0.57	Extreme ¹	Terrestrial	95.0
Cercopithecoidea	–	10.1/6.7	0.66	Strong-Extreme	–	86.6
Hylobatids	Monogamy	9.1/8.4	0.94	Slight ¹	Arboreal	139
Gibbons	Monogamy	6.2/6/1	0.97	Slight ¹	Arboreal	130
Siamangs	Monogamy	6.2/6/1	0.97	Slight ¹	Arboreal	147
Great apes	–	84.3/49.7	0.59	Mod-Strong ¹	–	116
<i>Pongo</i> spp.	Solitary	78.2/35.7	0.46	Strong ¹	Arboreal	139
<i>Gorilla</i> spp.	Female-choice	166/90	0.55	Strong ¹	Terr/Arb	116
<i>Pan troglodytes</i>	Fission-fusion M-B	48.4/39.3	0.81	Moderate ^{1,2}	Arb/Terr	105
<i>Pan paniscus</i>	Fission-fusion F-B	45.0/33.2	0.73	Moderate ^{1,2}	Arb/Terr	102
<i>Proconsul</i>	F-B	12.0/9.8 ⁴	0.82	Strong ³	Arboreal	~96.4 ⁶
<i>africanus/heselsoni</i>						
<i>Proconsul nyanzae</i>	F-B	40.4/30.0 ⁴	0.74	Strong ³	Arboreal	~95–100 ⁷
<i>Proconsul major</i>	F-B	86.7/63.4 ⁴	0.73	Strong ³	Arboreal	~95–100 ⁷
<i>Sivapithecus indicus</i>	Female-choice?	40/22 ⁵	0.55	Strong ³	Terrestrial	Unknown
<i>Ouranopithecus</i>	Female-choice?	100/50 ⁸	0.50	Strong ³	Terrestrial	Unknown

IMI, inter-membral index.

¹Plavcan (2001).²Kelley (1995a).³Kelley (1995b).⁴Rafferty et al. (1995); calculated assuming each sample is half male and half female.⁵DaSilva et al. (2010).⁶Rose (1993).⁷Ward (2007).⁸Estimated.

proximity to them. Three different genera are particularly widespread and successful, each containing 10 or more species (Table 1): *Ptilocolobus* (red colobus); *Trachypithecus* (leaf monkeys); and *Presbytis* (langurs).

Colobines are distinguished by a diet that is rich in mature and immature leaves (hence the appellation 'leaf monkeys' for some of them), but for most species unripe fruit is also a vital component of their diet; miscellaneous foliage and (for some) seeds may also be important (Clutton-Brock & Harvey, 1977a,b; McKey et al. 1981; Davies & Oates, 1995; Fleagle, 2013). High-crowned, high-cusped, saw-tooth like bilophodont cheek-teeth effectively shred unripe fruit, cellulose-rich mature leaves and other foliage into a finely comminuted digestible slurry. Colobines have less prognathic faces and more robust jaws than cercopithecines, morphology widely regarded as adapted to heavy mastication, even though jaw shape and robusticity are not related to food item toughness in any simple way (Daegling & McGraw, 2001). Colobine incisors are small, an adaptation to leaf-eating; leaves are conveyed to the cheek-teeth with less need for incising than fruits

(Hylander, 1975; Kay & Hylander, 1978; Davies & Oates, 1995). The partitioned or sacculated stomachs of colobines define several fermenting chambers, facilitating the digestion of cellulose by a co-evolved microbiota (Kuhn, 1964). Their diet is high not only in cellulose but also in tannins (Hladik, 1978) and alkaloids (Kay, 1978), to which their robust detoxifying physiology affords them tolerance (Chivers & Hladik, 1980; Andrews, 1981; McKey et al. 1981; Wrangham & Waterman, 1983).

Colobine positional behavior is a study in contrasts (Fig. 1; Table 3). Half of their activity consists of sitting in the central portion of the tree crown as they engage in extended, tranquil feeding bouts that are often followed by long periods of 'useful resting' during which time they digest their high-cellulose, high-secondary compound diet (Davies & Oates, 1995). Periods of inactivity are occasionally interrupted by loud, long-distance vocal exchanges among groups. Immobile periods are punctuated by movement that includes dramatic, long-distance leaps that can cover 10 times the body length. Compared with other cercopithecoids, colobines have wide interorbital distances, which

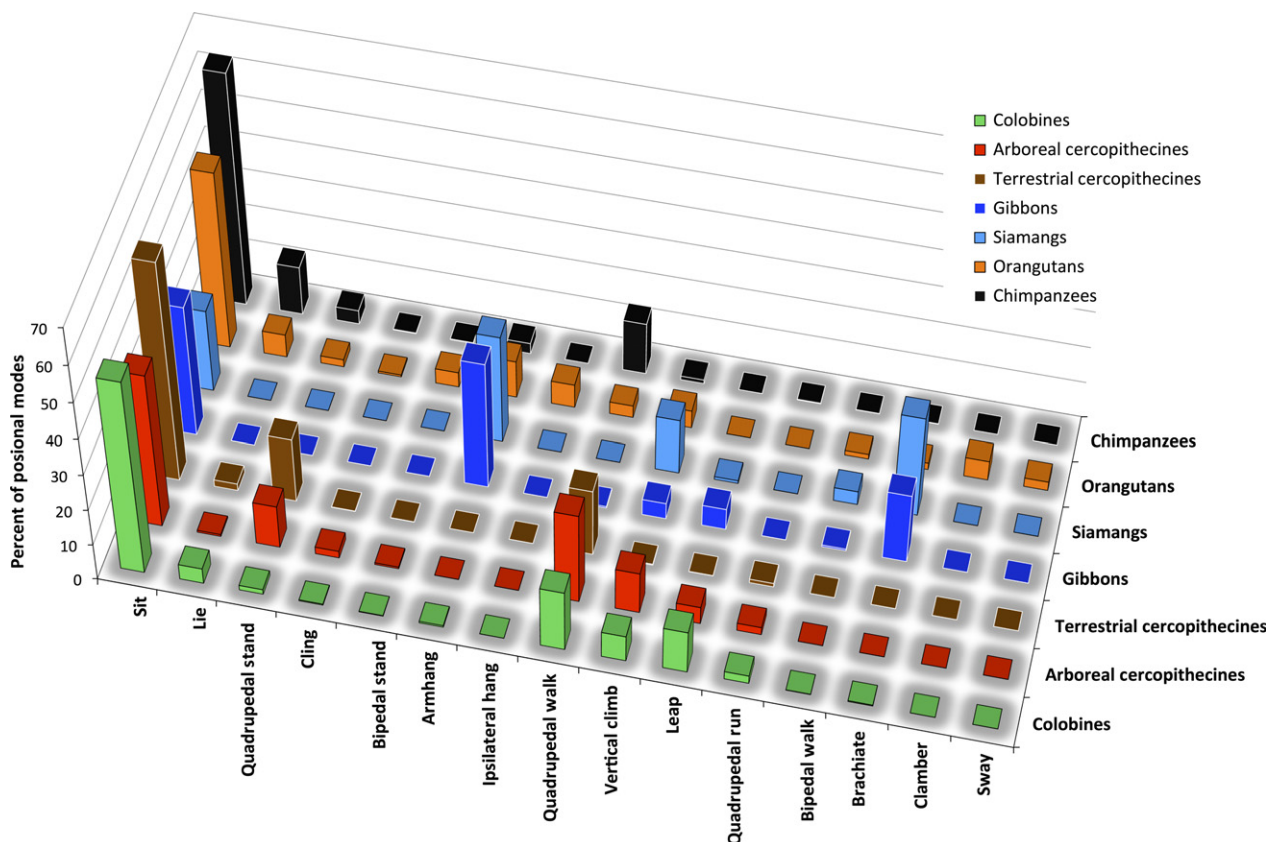


Fig. 1 Positional behavior among Old World monkeys and apes. Only studies that provided both arboreal and terrestrial (if applicable) data in all contexts are reviewed. Bipedalism is most common among siamangs and orangutans. Monkeys have high frequencies of walking, vertical climbing, leaping and running. Angle of support was not often precisely recorded in descriptions of climbing, but there is some suggestion that monkeys less often climb truly vertical supports than apes and utilize a different kinematic. Olive baboons at Gombe (Hunt, 1992a) vertical climb using a modified leaping ('pulse climb' in Hunt, 1992a) wherein the hindlimbs in concert propel the body upward and the arms are rapidly raised in concert to grasp the support higher up, after which the hindlimbs are flexed in preparation for the next 'pulse'. This type of vertical climbing contrasts to the hand-over-hand climbing of chimpanzees, which is much like a human climbing a ladder. Asian apes engage in much more brachiation than African apes. Orangutans commonly engage in two locomotor modes that are rare among other species: 'sway' and 'clamber'. The sway mode begins in a clinging posture after which the individual shifts its body weight so as to cause a compliant vertical support to oscillate back and forth until a target support comes within reach, after which a suspensory mode is used to transfer weight to the new support. Swaying is a means of travel that is less than half as costly as leaping (Thorpe et al. 2007a). Clamber involves forelimb suspension aided by often completely abducted hindlimbs. Chimpanzees are specialized for vertical climbing, arm-hanging and other torso-orthograde suspensory behaviors.

may improve depth perception, an advantage in judging landing spots at the end of leaps, when velocities are high (Hunt & Borniger, in prep.). Within tree crowns colobines locomote as above-branch, palmigrade quadrupedal walkers, occasionally shifting to a 'bounding' locomotion, a hopping-like gait consistent with high inter-membral index (IMI; i.e. percent of forelimb length relative to hindlimb length) and other anatomy evolved for leaping (see below; Fleagle, 1978; McGraw, 1998a,b).

While all cercopithecoids, even terrestrial cercopithecines, are adept at leaping and evince anatomical features evolved for leaping (Fig. 1; Table 3; Schultz, 1970), colobines have the most highly specialized anatomy adapted to this behavior (Fig. 2; Table 3; Ashton & Oxnard, 1964a,b). A classic comparison of two leaf monkeys, one of which leapt

more than the other (Stern, 1971; Fleagle, 1976a, 1977) helped to identify leaping morphology: long hindlimbs (IMI = 81.4; Fig. 2; Table 2); long lumbar vertebral segments of up to seven vertebrae; powerful erector spinae muscles, particularly the lumbar muscles (Fleagle, 1977); and long feet. The kinematics of leaping begin with spine, hip, knee and often ankle strongly flexed, after which each is violently extended to accelerate into take-off. The femur of leapers has a proximally extended greater trochanter, which serves to increase the moment arm of the gluteal muscles (Fig. 2; Fleagle, 1976a), thus allowing greater moments around the hip joint and greater velocity. Longer hindlimb segments increase the time over which force is applied to the take-off support, thus increasing final velocity, which in turn increases the length of the leap (Fleagle, 1976a, 1977;

Table 3 Positional behavior in superfamilies Cercopithecoidea and Hominoidea.

Species	Sit	Lie	Quad. stand	Squat	Cling ¹	Biped stand	Arm- hang	Ipsilateral suspend	Quad. walk	Vertical climb ²	Leap ³	Quad. run ⁴	Bipedal walk	Brachiate ⁵	Clamber	Suspensory	Transfer ⁶	Sway ⁷	N
<i>Presbytis</i>																			975
<i>obscura</i> ⁷	39.4	0.0	0.0	0.0	0.0	0.0	0.8	0.0	34.5	7.3	17.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts, 300 h
<i>Presbytis</i>																			1267
<i>melalophos</i> ⁷	22.1	0.0	0.0	0.0	0.0	0.0	2.1	0.0	36.8	10.4	26.5	0.0	0.0	2.1	0.0	0.0	0.0	0.0	bouts, 500 h
<i>Rhinopithecus</i>																			20 131
<i>roxellana</i> ⁸	79.4	0.4	5.1	0.0	0.0	0.0	0.0	0.0	9.2	2.5	2.8	0.2	0.0	0.2	0.0	0.0	0.1	0.0	surveys
<i>Colobus</i>																			4782
<i>guereza</i> ⁹	67.6	10.9	0.9	0.0	1.3	0.8	1.0	0.0	5.6	2.9	5.6	1.2	0.7	0.0	0.0	0.2	0.0	0.0	surveys
<i>Colobus</i>																			6452
<i>guereza</i> ¹⁰	31.1	2.9	1.4	0.0	0.0	0.0	0.0	0.0	26.3	10.3	27.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts
<i>Colobus</i>																			5539
<i>angolensis</i> ¹¹	83.3	8.9	0.7	0.0	0.0	0.0	0.0	0.0	3.1	0.8	1.1	1.7	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>Colobus</i>																			3413
<i>polykomos</i> ¹²	65.4	6.7	0.1	0.0	0.6	0.0	0.0	0.0	11.2	3.8	3.9	7.9	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>Procolobus</i>																			1589
<i>verus</i> ¹²	61.7	5.1	0.9	0.0	0.2	0.0	0.2	0.0	14.5	3.8	6.5	7.2	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>Ptilocolobus</i>																			7515
<i>badius</i> ¹⁰	30.7	0.3	2.7	0.0	0.0	0.3	0.0	0.0	24.4	23.0	17.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts
<i>Ptilocolobus</i>																			4156
<i>badius</i> ¹²	56.3	6.7	0.9	0.0	0.4	0.0	0.0	0.0	18.7	6.0	6.3	2.9	0.0	0.0	0.0	1.4	0.0	0.0	surveys
<i>Colobines</i>																			
	53.7	4.2	1.3	0.0	0.2	0.1	0.4	0.0	16.6	7.1	11.6	2.1	0.1	0.2	0.0	0.2	0.0	0.0	
<i>Cercopithecus</i>																			3461
<i>diana</i> ¹²	32.9	0.6	12.2	0.0	8.4	0.0	0.0	0.0	26.6	10.7	5.7	6.0	0.0	0.0	0.0	0.1	0.0	0.0	surveys
<i>C. mitis</i> ¹⁰																			6444
	30.1	0.9	15.1	0.0	0.0	1.4	0.0	0.0	28.6	18.5	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts
<i>C. ascanius</i> ¹⁰																			6450
	30.4	0.0	11.3	0.0	0.0	1.7	0.0	0.0	22.1	24.4	10.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts
<i>C. campbelli</i> ¹²																			1434
	41.4	0.6	12.8	0.0	2.8	0.0	0.0	0.0	30.2	6.0	2.2	3.2	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>C. petaurista</i> ¹²																			2042
	61.4	0.7	9.7	0.0	2.3	0.0	0.0	0.0	15.4	4.7	2.5	2.5	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>C. aethiops</i> ¹³																			10 h
	68.0	0.0	12.0	0.0	0.0	0.0	0.0	0.0	17.3	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Cercocebus</i>																			1320
<i>atys</i> ¹²	52.3	0.0	10.2	0.0	1.2	0.0	0.0	0.0	28.5	4.4	0.4	2.0	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>Lophocebus</i>																			6165
<i>albigena</i> ¹⁰	24.1	1.1	11.0	0.0	0.4	0.4	0.0	0.0	29.8	22.2	10.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	bouts
<i>Arboreal</i>																			
<i>cercopiths</i>	42.6	0.5	11.8	0.0	1.9	0.4	0.0	0.0	24.8	11.4	4.7	2.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Papio</i>																			11.7 h
<i>anubis</i> ¹³	72.8	0.0	12.9	0.0	0.0	0.0	0.0	0.0	12.9	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Papio</i>																			2087
<i>anubis</i> ¹⁴	57.1	3.2	14.5	0.2	0.3	0.0	0.0	0.0	23.2	0.5	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	surveys
<i>Papio</i>																			118.0 h
<i>anubis</i> ¹⁵	52.1	2.3	25.5	0.0	0.0	0.2	0.0	0.0	18.7	0.2	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Terrestrial</i>																			
<i>cercopiths</i>	60.7	1.8	17.6	0.1	0.1	0.1	0.0	0.0	18.3	0.2	0.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Hylobates</i>																			742
<i>agilis</i> ¹⁶	36.6	0.0	0.0	0.0	0.0	0.0	19.3	0.0	1.5	2.8	10.6	0.0	0.0	29.3	0.0	0.0	0.0	0.0	surveys
<i>Hylobates</i>																			873
<i>agilis</i> ¹⁷	46.3	0.0	0.0	0.0	0.0	0.0	28.8	0.0	0.0	1.5	2.2	0.0	0.2	21.1	0.0	0.0	0.0	0.0	surveys
<i>Hylobates</i>																			873
<i>lar</i> ¹⁸	29.1	0.0	0.0	0.0	0.0	0.0	46.7	0.0	0.0	8.6	2.3	0.0	1.3	12.4	0.0	0.0	0.0	0.0	bouts, 50 h
<i>Hylobates</i>																			33 740
<i>hainanus</i> ¹⁹	32.5	0.0	0.0	0.0	0.0	0.0	44.7	0.0	0.0	4.6	8.0	0.0	0.2	13.4	0.0	0.0	2.4	0.0	obs
<i>Gibbons</i>																			
	36.1	0.0	0.0	0.0	0.0	0.0	34.9	0.0	0.4	4.4	5.8	0.0	0.4	19.0	0.0	0.0	0.6	0.0	

Table 3 (continued)

Species	Sit	Lie	Quad. stand	Squat	Cling ¹	Biped stand	Arm- hang	Ipsilateral suspend	Quad. walk	Vertical climb ²	Leap ³	Quad. run ⁴	Bipedal walk	Brachiate ⁵	Clamber	Suspensory	Transfer ⁶	Sway ⁷	N
<i>Hylobates</i>																			2582
<i>syndactylus</i> ¹⁸	20.4	0.0	0.0	0.0	0.0	0.0	32.9	0.0	0.0	25.4	1.5	0.0	2.2	17.7	0.0	0.0	0.0	0.0	bouts, 800 h
<i>Hylobates</i>																			442 obs
<i>syndactylus</i> ²⁰	24.9	0.0	0.0	0.0	0.0	0.0	26.5	0.0	0.0	4.8	0.0	0.0	5.2	37.6	0.0	0.0	1.5	0.0	
<i>Siamangs</i>																			
	22.7	0.0	0.0	0.0	0.0	0.0	29.7	0.0	0.0	15.1	0.8	0.0	3.7	27.7	0.0	0.0	0.8	0.0	
<i>Pongo</i>																			18 220
<i>pygmaeus</i> ²¹	55.6	4.0	1.1	0.0	0.8	3.8	12.4	6.9	1.3	2.4	0.0	0.0	0.5	1.8	6.5	0.8	0.0	3.1	surveys
<i>Pongo abelli</i> ²²																			9961
	41.8	8.6	2.9	0.3	0.1	4.3	8.0	5.8	5.2	7.2	0.0	0.0	2.0	1.7	4.0	4.5	1.7	1.7	surveys
<i>Orangutans</i>																			
	48.7	6.3	2.0	0.2	0.5	4.1	10.2	6.4	3.3	4.8	0.0	0.0	1.3	1.8	5.3	2.7	0.9	2.4	
<i>Pan</i>																			16 303
<i>troglodytes</i> ¹⁴	62.4	12.1	2.5	0.7	0.3	0.3	4.4	0.0	16.1	0.9	0.0	0.3	0.1	0.1	0.0	0.1	0.2	0.0	
<i>Pan</i>																			10 077
<i>troglodytes</i> ²³	65.1	14.5	5.0	0.0	0.0	0.1	1.3	0.0	12.1	−1.1	0.0	0.0	0.1	0.1	0.0	0.0	−0.3	0.0	bouts
<i>Chimpanzees</i>																			
	63.8	13.3	3.8	0.4	0.2	0.2	2.9	0.0	14.1	1.0	0.0	0.2	0.1	0.1	0.0	0.1	0.2	0.0	

¹Also including 'stand/forelimb suspend' of McGraw (1998a,b).

²Also including 'bimanual pull-up' of Gebo & Chapman (1995).

³Also including vertical bound for *Rhinopithecus* and drop for *Pongo*.

⁴Also including horizontal bound.

⁵Brachiate only for apes; arm-swinging for cercopithecoids.

⁶Also including tree sway and ride for *Pongo*, ride for *Rhinopithecus*.

⁷Fleagle (1978); values represent percentage of all positional bouts; focal individual, continuous sampling; site: Selangor, West Malaysia; 18.3% of quadrupedal progression was 'hop'; no other species in table hops.

⁸Zhu et al. (2015); values represent percentage of 1-min instantaneous focal sample on adults in all contexts; site: Zhouzhi Nature Reserve, China.

⁹Morbeck (1977); values represent percentage of 10-s instantaneous scan samples; site: Limura, Kenya.

¹⁰Gebo & Chapman (1995); percentage of total positional bouts, continuous random focal sampling; site: Kibale Forest, Uganda.

¹¹Dunham (2015); percentage of total positional bouts, rotating instantaneous focal sampling of adults in all contexts; site: Diana Forest, Kenya.

¹²McGraw (1998a,b); percentage of instantaneous focal sampling in all contexts; site: Tai Forest, Ivory Coast.

¹³Rose (1974); percentage of minutes observed, continuous scan sampling during feeding only; site: Murchison Falls, Uganda.

¹⁴Hunt (1989); percentage of 2-min instantaneous focal sampling standardized by hour of day; midsex; adults only; site: Gombe, Tanzania.

¹⁵Rose (1977); percentage of time in each behavior; continuous half hour focal observation; adults only; midsex average; site: Gilgil, Kenya.

¹⁶Gittins (1983); percentage of 10-min instantaneous scan surveys; site: Sungai Dal, West Malaysia.

¹⁷Srikosamatara (1984); percentage of 5-min instantaneous scan surveys; site: Khao Yai, Thailand.

¹⁸Fleagle (1976b); percentage of all positional bouts; focal individual, continuous sampling; site: Pahang, West Malaysia.

¹⁹Fan et al. (2013); Fan et al. submitted; percentage of observations during feeding only for posture; percentage of observations in all contexts for locomotion; instantaneous scan of social group at 5-min intervals; site: Bangliang Nature Reserve, China.

²⁰Chivers (1972); percentage of instantaneous scan surveys; site: Ulu Sempam, Malaysia.

²¹Manduell et al. (2011) and Manduell KL (personal communication); percentage of 1-min instantaneous focal samples; adults; site: Sabangau, Indonesia; 'arm-hanging' = pronograde suspend + postural bridge + orthograde forelimb suspend + orthograde quadrumanous suspend; 'suspensory' = bridge + torso-pronograde suspension + drop.

²²Thorpe & Crompton (2005, 2006); percentage of positional bouts, 1-min instantaneous focal sampling; site: Gunung Leuser, Sumatra, Indonesia.

²³Doran (1996); percentage of positional bouts, continuous focal sampling; site: Tai, Ivory Coast.

Preuschoft et al. 1979); while colobines have longer hindlimbs than other cercopithecoids, specialized leapers such as tarsiers and indriids have still longer hindlimbs (Preuschoft et al. 1993). Muscles that have an origin on the

femur and insert on the patella, the vasti, are larger in leapers; they drive the powerful knee extension required in leaping (Stern, 1971; Fleagle, 1976a). The larger femoral fibers of flexor cruris lateralis (biceps femoris) increase the

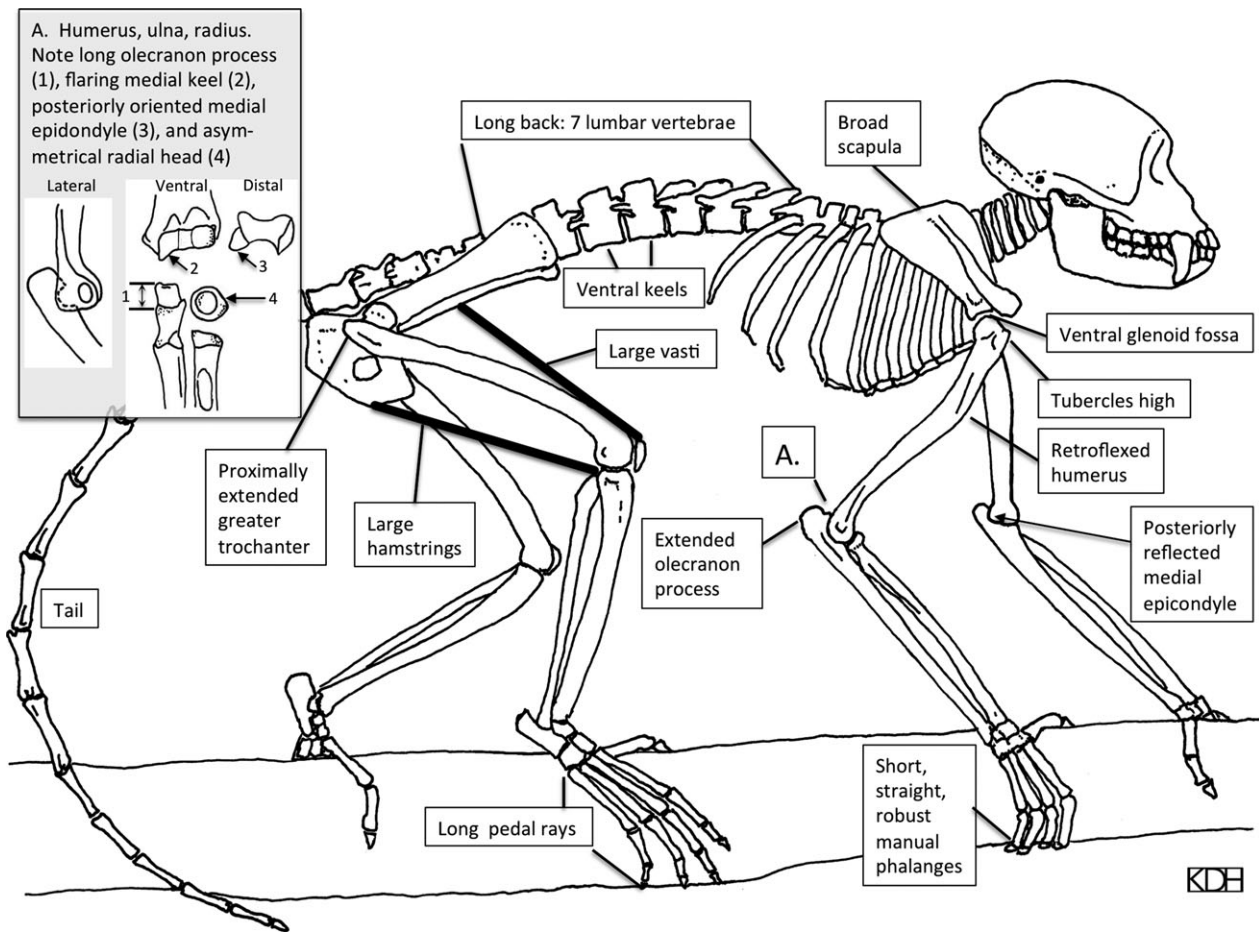


Fig. 2 Specializations of a generalized Old World monkey. Hindlimbs slightly longer than forelimbs, long muscular backs, long pedal rays, long moment arms for muscles that extend the hip, and large hamstrings and vasti are leaping adaptations. Monkeys sleep sitting and often feed sitting; fibrous ischial pads are an adaptation to this posture. After Fleagle (2013), Rose (1993) and specimens in the Human Origins and Primate Evolution Laboratory, Indiana University.

power of hip extension (Fleagle, 1977; Table 2), and a more proximal insertion of gracilis and semitendinosus muscles serves a similar function.

Long, gap-crossing leaps often result in a distance covered in descent as great or greater than the horizontal distance covered. As the leaper lands, the forelimbs bear much of the deceleration effort, particularly the vertical descent component, and braking often ends with the individual in a bimanual arm-hanging position. Thus, in colobines adaptations for leaping also selected for shoulder mobility and forelimb suspensory traits (Ashton & Oxnard, 1963, 1964a,b; Napier, 1963; Oxnard, 1963, 1967; Ashton et al. 1965). After landing, the semi-arm-hanging posture requires a 'pull-up' or hoist to attain a sitting or standing position. If the landing substrate is compliant, which is common, the support deforms to near-vertical under the weight of the leaper and instead of a hoist the landing is followed immediately by a bounding climbing, angled-ascent walking or less often a hand-over-hand vertical climbing.

Arboreal cercopithecines

The arboreal cercopithecines (all members of the tribe Cercopithecini plus the macaques and mangabeys, not including *Erythrocebus*, *Papio*, *Mandrillus* or *Theropithecus*) consist of 48 species distributed across Asia and Africa. The mangabeys are a nomenclatural oddity in that they are polyphyletic. West African mangabeys ('mandrillan mangabeys' in Table 1) are phylogenetically closer to the drills and mandrills with which they are sympatric than they are to the East African mangabeys ('papionan mangabeys'), which are more closely related to olive or savanna baboons (Cronin & Sarich, 1976; Disotell et al. 1992; Fleagle & McGraw, 1999). Mangabeys have converged on non-papionan cercopithecines in ecology, anatomy and arboreality (Chalmers, 1968; Struhsaker & Leland, 1979; Hill, 1984), and consequently they are pooled here with the arboreal cercopithecines. Likewise, macaques are phylogenetically closer to the papionan tribe than to the cercopithecine tribe (Table 1), but

their greater arboreality warrants pooling with arboreal cercopithecines for this discussion.

The arboreal cercopithecines are smaller than the colobines, with female body masses ranging between 1.1 (the Angolan talapoin, *Miopithecus talapoin*) and 12.8 kg (the Tibetan macaque, *M. thibetana*), averaging 6.1 kg (Table 1; abstracted from Fleagle, 2013). Arboreal cercopithecines live in multifemale groups, many of which have only a single male (Cords, 2000, 2012); they are all female-bonded (Wrangham, 1980; Smuts et al. 1986; Sterck et al. 1997; Cords, 2012). Mean sexual dimorphism is 64%, even greater than that of colobines.

Two genera are extraordinarily successful, the Asian macaques (20 species) and the African genus *Cercopithecus* (guenons; 26 species). In Asia the macaques fill both the arboreal and terrestrial niches, niches that are divided between more specialized terrestrial and arboreal cercopithecines in Africa. Although some species of macaque are quite terrestrial, all are dependent on trees for food and devote a large proportion of their daily activity budget to arboreal activities; all sleep in trees (Whitehead & Jolly, 2000).

The arboreal cercopithecine diet is high in unripe and ripe fruit, supplemented most often by insects, blossoms and new leaves (Whitehead & Jolly, 2000; Cords, 2012; Fleagle, 2013); they have flatter, lower, rounder-cusped teeth than colobines, an adaptation to frugivory (Kay, 1978). Many food items, particularly unripe fruits, require incising before mastication, resulting in extensive incisal wear; to compensate for this wear cercopithecines have, compared with colobines, large incisors; incisor breadth is correlated with the average fruit diameter in the diet (Kay & Hylander, 1978).

Arboreal cercopithecine forelimbs are slightly shorter than their hindlimbs, giving them an IMI of 87.0 (Table 2; Fleagle, 2013). Arboreal cercopithecines are more active than colobines, spending less time sitting and lying and more time walking and climbing (Table 3); they stand more often because they frequently pause to observe others, scan the habitat or wait on other group members. They are graceful, quick and competent above-branch walkers when moving within a tree canopy, and accomplished leapers when moving between tree crowns. They typically sit to feed but shift location often in brief locomotor bouts, often feeding only briefly at any one site – at times plucking food items almost without slowing, storing food in their cheek pouches to be masticated and swallowed later. The overall effect might be described as restless.

Arboreal cercopithecines walk and run more and leap less than colobines (Fig. 1; Table 3). Muscle groups used more often during quadrupedal walking are those that originate on the pelvis and insert on the tibia. This two-joint-crossing morphology affords the muscles double duty during the propulsive phase of walking. These muscles, gracilis, semimembranosus and semitendinosus, and crural fibers of

the biceps femoris, retract the thigh while either flexing the knee or maintaining it as slightly flexed, the principal action in the propulsive phase of walking (Fleagle, 1977). Distal insertion of sartorius onto the crus allows flexure of the thigh during the recovery phase of walking (Fleagle, 1977).

Terrestrial cercopithecines

Some 10 species of cercopithecoid in the genera *Erythrocebus* (patas monkeys), *Papio* (baboons), *Mandrillus* (mandrills) and *Theropithecus* (geladas) are adapted to terrestrial and/or open habitats; all are confined to Africa and a small part of the Arabian Peninsula. This econiche is both relatively recent (Fleagle, 2013) and atypical of the monkeys. The terrestrial cercopithecines are much heavier than arboreal cercopithecines, with female body masses ranging from 8.7 to 15.4 kg, with a mean of 12.0 kg (body masses from Fleagle, 2013). They are larger both because they need not retain mobility in trees and because large body size is energetically efficient for long-distance terrestrial travel. Sexual dimorphism is the greatest of the Old World monkeys, averaging 49%; accordingly, dominance rank is highly determinant of reproductive success (Strum, 1982; Altmann et al. 1996). Terrestrial species are to a great extent allometrically scaled up versions of arboreal cercopithecines. They have long backs, large back muscles and other morphology related to leaping and walking, as described above. They are comfortable in trees, even though some species are nearly completely terrestrial, and where their habitat includes trees they obtain much of their nutrition from arboreal resources (Whitehead & Jolly, 2000) where they presumably must compete with sympatric apes.

Erythrocebus patas is restricted to open habitats and has little overlap with chimpanzees, though agonism and thus competition can be substantial where they are coincident (Pruetz & Marshack, 2009). Savanna baboons overlap with chimpanzees in many habitats and rely on many of the same foods (Peters & O'Brien, 1981); fully 90% of the fruit species utilized by chimpanzees are also utilized by baboons (Matsumoto-Oda & Kasagula, 2000). The greater population density of papionins compared with apes and the similarity of their diets and body masses suggest significant competition and indeed at sites such as Gombe where baboons are abundant the two can be seen feeding in the same trees. Mandrills and drills are sympatric with western chimpanzees (Tuttle, 1986; Matthews & Matthews, 2002) and likely they compete for shared food resources in a similar fashion. *Theropithecus* is restricted to the highlands of Ethiopia and does not overlap with apes, although their paleodistribution was pan-African, suggesting that paleospecies competed with apes analogously to extant baboons. *Papio hamadryas* is confined to extremely dry habitats and likewise is not sympatric with apes.

Most terrestrial cercopithecines are female-bonded (Smuts et al. 1986; Sterck et al. 1997; Cords, 2012), but in

the extreme desert and montane habitats in which they are found hamadryas baboon (*P. hamadryas*) and mountain baboon (*P. ursinus*) females do not form close bonds, and like apes disperse as they reach late adolescence or early adulthood (Byrne et al. 1990; Jolly, 2001). These species are organized in multi-level societies built up from one-male/multifemale breeding units (sometimes called 'harems') that are imbedded in larger social groups that may reach into the hundreds. Hamadryas baboon males form bonds with other breeding unit males to yield a multilevel society with principle bonds between a male and the females in his breeding unit, and weaker but still important bonds among males so that three one-male units aggregate into clans; in a further layering there are still weaker bonds among clans, ultimately making up a large band (Jolly, 2001). This male-bonding is important both because it is otherwise only seen among apes (chimpanzees and mountain gorillas) and because there appears to be relationships between low-productivity environments and the breakdown of female bonding.

When food resources are rich enough and clumped enough to allow a group of females to effectively defend a feeding site, female bonds form (Wrangham, 1980). Apes lack female bonds because ripe fruits are sparse and dispersed (Wrangham, 1979); it might be expected that on an evolutionary timescale chimpanzees transitioned from female-bonded to fission-fusion social organization when sympatric monkeys reached a population density high enough to deplete food resources to the extent that feeding sites could no longer be defended by females. As is the case among gorillas, hamadryas females are most closely bonded to a breeding male. Among mountain gorillas (though not lowland gorillas), two related males may be found in a social group, each bonded to different females and each responsible for group defense against outsider males (Harcourt & Stewart, 2007). As discussed below, there is evidence that the common ancestor of gorillas, chimpanzees and human was gorilla-like, and some argue their social system may have been hamadryas-like (Swedell & Plummer, 2012), a system not dissimilar to that of gorillas.

Extant Old World monkey functional morphology

Compared with hominoids, cercopithecoids are small; their body mass averages 8.4 kg (males 10.1 kg, females 6.7 kg); their small size means supports on which they move are relatively large and stable (Morbeck, 1977; Rose, 1978, 1979; Hunt, 1992a). They walk and run nimbly and confidently in trees compared with clumsier arborealists such as squirrels. Cercopithecoids are anatomically 'uniform' (Schultz, 1970) enough, despite specializations, that abstracting a generalized Old World monkey morphology provides insight into the adaptation of the entire group. In accord with their anatomy (Schultz, 1970), monkeys have less diversity in their

positional repertoire than apes. This consistency extends to their ascension of trees: as discussed above, their typical vertical climbing behavior is kinematically similar to either two-footed leaping or quadrupedal walking.

Old World monkeys are anatomically specialized to engage in four positional modes, arboreal walking on relatively large supports, terrestrial walking, running and leaping (Fig. 2; Table 4; Schultz, 1930, 1936, 1953, 1961, 1963, 1970; Miller, 1932; Oxnard, 1963, 1967; Ashton & Oxnard, 1964a; Ripley, 1967, 1979; Lewis, 1969; Jenkins, 1973; Roberts, 1974; Rose, 1974, 1978, 1979, 1988a,b, 1989, 1994; Fleagle, 1976a,b, 1977, 1978, 1983; Morbeck, 1977; Fleagle & Simons, 1978, 1982; Szalay & Dagosto, 1980; Tardieu, 1981; Harrison, 1982, 1987, 1989; Fleagle & Kay, 1983; Sarmiento, 1983, 1985, 1987, 1988, 2000; Aiello & Dean, 1990; Schmitt, 1998, 1999; Larson, 2015). While each mode has its unique anatomical demands, each of the four requires rather stereotyped parasagittal limb excursions and adaptations for stability and efficiency rather than flexibility (Jenkins, 1973; Rose, 1993).

As discussed above, long hindlimbs, a proximally extended greater trochanter, large vasti and large hamstrings function to powerfully extend the hip and knee during leaping. Monkeys have long backs, possessing seven lumbar vertebrae vs. five or four in apes and humans, and backs are extended further by taller vertebral bodies compared with apes (Schultz, 1961; Ankel, 1967; Benton, 1967). A long, flexible, powerful back serves the same function as long hindlimbs, allowing a longer period of acceleration during leaping, and thus a higher velocity and longer leap (Napier & Napier, 1967; Ripley, 1967; Fleagle, 2013). While hindlimbs are slightly longer than forelimbs, monkeys differ from highly specialized leapers such as *Indri*, which have hindlimbs much longer in relation to body mass than monkeys; instead they exhibit a compromised morphology. Compared with specialized leapers and mammalian cursors, monkeys have short arms and legs in relation to their body mass. Short limbs lower the center of gravity and allow for better balance on unstable arboreal supports (Schmitt, 1994, 1998; Schmitt et al. 2010), while a long back (rather than exceptionally long hindlimbs) increases contact time during takeoff without compromising balance.

Monkey vertebrae have a ventral keel, a ridge running from top to bottom with a concavity on each side (Schultz, 1961; Harrison, 1986). This keel is an adaptation to leaping. When the lumbar vertebrae are flexed in preparation for a leap, the ventral edges of adjacent vertebrae are in closer proximity than normal; when the back extensor muscles contract they create moments that rotate the vertebrae as the back extends. The contraction of the dorsally placed erector spinae muscles exerts compressive forces on the ventral edge of the vertebra as they compress the intervertebral disks, producing the moments that extend the back. A ventral keel is a reinforcement of the area where the greatest compressive forces are concentrated. The monkey thorax

Table 4 Distinctive Old World monkey traits and their likely function.

Feature	Function	Positional mode implicated
Hindlimbs slightly longer than forelimbs	Increase contact with support during acceleration	LE
Arms, legs short	Maintain balance on unstable support	ARW
Short fingers	Optimal balance of grip, efficiency	ARW/TW
Less robust, straight phalanges	Resist forces both during gripping, digitigrady	ARW/TW
Robust, partly opposable thumb	Food processing, gripping	ARW?
Large ulnar styloid, carpal articulation	Stabilize wrist	ARW/TW/LE
Asymmetrical radial head	Stabilize elbow in full pronation	ARW/TW/LE
Elongated olecranon process of ulna	Increase moment arm for triceps	LE
Shallow olecranon fossa	Allows bony support of elbow joint during suspension	AH
Posteriorly reflected medial epicondyle	Increase moment arm of digital flexors for elbow extension during 'toe' off	Running, LE
Proximally placed humeral tubercles	Increase moment arms of rotator cuff muscles	ARW/TW/LE
Small humeral head	Joint stability in parasagittal movement	ARW/TW/LE
Broad bicipital groove	No need for shoulder mobility	ARW/TW/LE
Retroflexion of proximal humerus	Function unclear	ARW/TW, LE?
Narrow, pear-shaped glenoid	Joint stability in parasagittal movement	ARW/TW/LE
Dorsoventrally deep, narrow ribcage	Decrease bending moments on spine, hip, knee	ARW/TW/LE
Straighter ribs	Decrease bending moments on spine, hip, knee	ARW/TW/LE
Short clavicle	Consequence of narrow torso	ARW/TW/LE
Humeral torsion	Consequence of narrow torso	ARW/TW/LE
Long lumbar vertebra segment	Increase contact with support during acceleration	LE
Narrow pelvis	Decrease bending moments on spine, hip, knee	ARW/TW/LE
Proximally extended greater trochanter	Increase moment arm of hip extensors	LE
Less abducted great toe	Aid lateral toes exerting force during extension	ARW/TW/LE
Long, pedal rays	Increase contact with support during acceleration	LE
Tail	Improve balance on unstable supports	LE/ARW
Large back muscles	Powerfully extend back to accelerate	LE
Large vasti, hamstrings	Powerfully extend hindlimbs, hip	LE
Bilophodont teeth	Masticate foliage, unripe fruit	

AH, arm-hanging; ARW, arboreal walking; LE, leaping; TW, terrestrial walking.

is deep and narrow (Schultz, 1936, 1950), a shape effected by ribs less tightly curved than those of apes. The narrow monkey thorax requires a shorter clavicle than the broad ape thorax. Humeral torsion, narrow pelvis and adducted great toes (Fig. 3) are features that provide stability and efficiency during parasagittal limb movements common during walking, leaping and running (Fig. 3; Table 4). A narrow body plan reduces moments on the shoulder or hip joints when the body is supported by ipsilateral limbs or by a single limb; such one-sided support is seen with single-footed leaping and pacing gaits. By reducing moments around joints and therefore the necessity to counter these forces with muscle action, a narrow body plan serves a muscle-sparing function.

The surface area of the femoral head of monkeys is small relative to that of apes, describing a hemisphere rather than a globe. The restricted femoral head is part of a functional complex that limits excursion and emphasizes stability at the expense of flexibility.

The humeral head is similarly restricted, and the bony attachments for the rotator cuff muscles, the humeral tubercles, extend proximally above the humeral head,

thereby providing greater moment arms for shoulder flexors but crowding the humeral head and impinging on the rim of the glenoid, limiting shoulder mobility (Fig. 2; Schultz, 1930; Tuttle, 1975; Corruccini et al. 1976; Harrison, 1987; Larson & Stern, 1989). The complementary scapular articulation is also smaller. In ventral view, monkeys have a narrow, pear-shaped scapular glenoid fossa that is somewhat trough shaped in lateral view; they lack adaptations for mobility seen in apes.

The distal humeral joint surface of monkeys is narrow and has a shallowly angled zona conoidea but a distinct medial flare of the trochlea (Fig. 2). The elongated olecranon process of monkeys increases the lever arm for triceps, allowing powerful elbow extension during leaping and quadrupedal walking and running. The longer lever arm limits elbow extension, as the process impinges on the humerus during extension. The process is reduced in apes to allow the complete extension necessary for arm-hanging and other suspensory behavior (Fig. 2). The complementary olecranon fossa is shallow, further restricting extension. The posteriorly oriented medial epicondyle of the monkey elbow (Fig. 2) displaces the origin of finger and wrist flexors

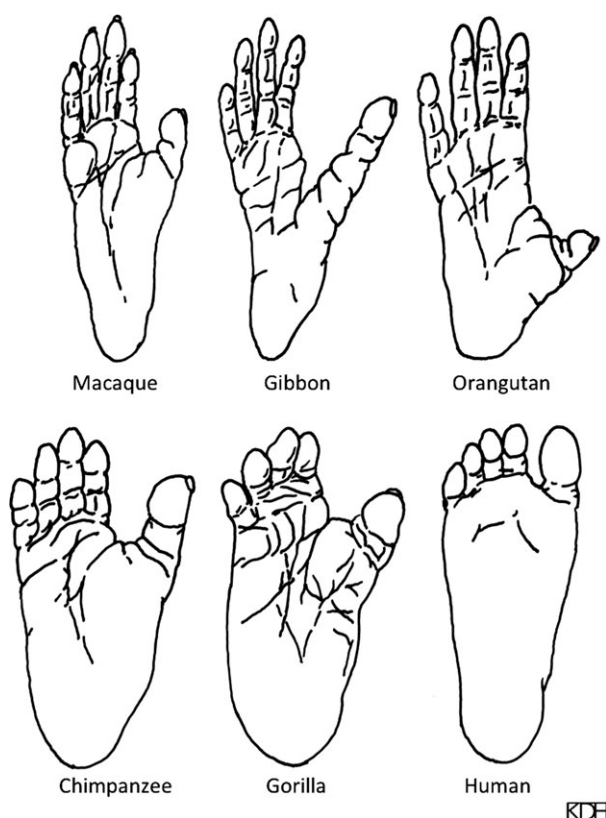


Fig. 3 Monkeys have less abducted great toes and therefore less pedal gripping capabilities, compared with apes. Gripping great toes are widely regarded as an adaptation for gripping vertical supports during vertical climbing. After Schultz (1950).

dorsally (i.e. posteriorly), and has been hypothesized to reduce medial rotatory torques in the habitually pronated forearm of monkeys (Jolly, 1972; Jenkins, 1973; Fleagle & Simons, 1982). Another possibility is that the posterior orientation increases the moment arm of the digital flexors during 'toe' off. During leaping or running as the fingers flex during the final push off they are fixed by contact with the substrate so that contraction of the finger and wrist flexors extends the elbow as well as flexing the digits. With the fingers relatively fixed, palmar and digital flexors

impose moments on the flexor origin on the humerus and the more posteriorly oriented the medial epicondyle is, the greater the moment arm for the flexors (Fig. 4).

The flared medial trochlear keel of monkeys resists a resultant force generated as the elbow extensors and digital flexors extend the elbow and digits. Because the digital flexors are medial to the humeroulnar articulation there is a resultant medially directed force that tends to medially rotate the ulna and dislocate the ulna medially. An angled medial trochlear flare resists this force (Fig. 5). An asymmetrical ventrolaterally flattened area on the radial head (Fig. 2) locks into a complementary ulnar articulation in the normal pronated position (Rose, 1988b). A large ulnar styloid process with an extensive complementary articulation with the carpus resists large loads during 'toe' off, the last instant of the support phase during running and leaping (Fig. 6; Lewis, 1965, 1969, 1972). The flattened radial head and the large ulnar styloid process with its robust carpoulnar articulation limit supination but provide stability; monkeys can rotate their wrists through only 90°, vs. ~150° for apes (Knussman, 1967; Tuttle, 1969, 1970; O'Connor & Rarey, 1979).

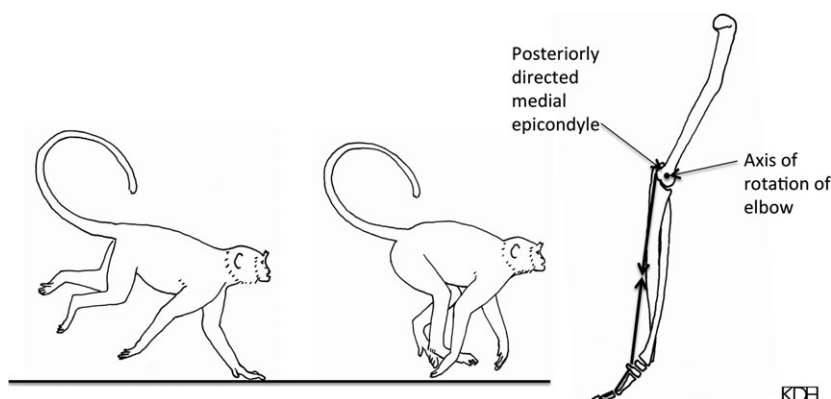
Monkey fingers and hands are short, and the metacarpals and phalanges lack ventral curvature (Schultz, 1930); monkeys are small in comparison to the tree branches on which they typically locomote, obviating the need for long fingers to grip substrates. Straight phalanges best resist forces in multiple planes and are typical of non-suspensory primates (Preuschoft et al. 1993). The monkey hallux is not as abductible as that of apes (Fig. 3) and the gap between the great toe and lateral toes is small, limiting their ability to grip large supports and reflecting their lesser dependency on hand-over-hand vertical climbing and its requisite gripping requirement.

A long tail functions to maintain balance on compliant supports (Buck et al. 1925), and thus is an adaptation to arboreal walking.

Extant ape ecomorphology and socioecology

There are five genera and 20 species of living apes (Table 1) falling into two major groups, the lesser apes and the great

Fig. 4 A posteriorly oriented medial epicondyle places the origin of the digital and wrist flexors farther from the axis of rotation of the elbow, increasing the moment arm of the flexors. These flexors cross two joints so that the action of the muscles is to both extend the elbow and flex the digits during the final moments of 'toe' off. Both running and leaping are believed to involve forceful flexion of the digits and wrist. After Rose (1979) and specimens in the Human Origins and Primate Evolution Laboratory, Indiana University.



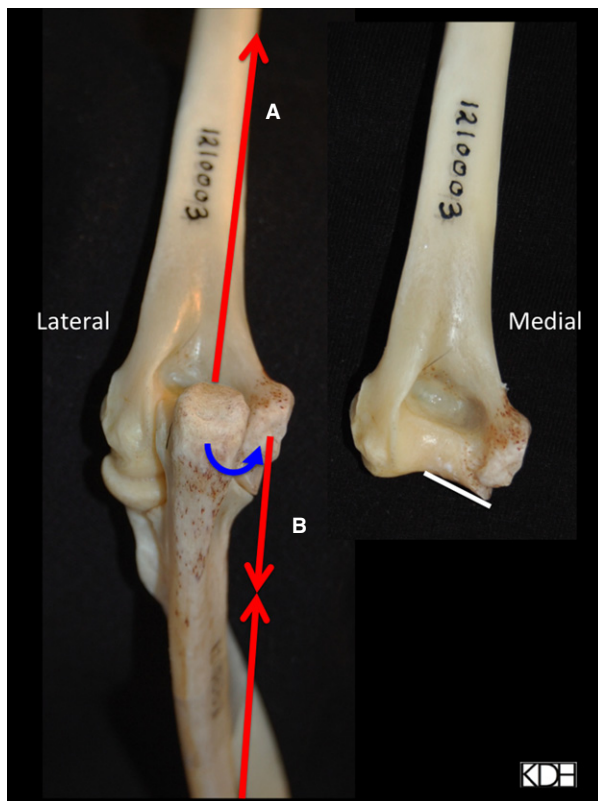


Fig. 5 Dorsal view of a *Trachypithecus* humerus, ulna and radius (left), and the same specimen with the ulna and radius disarticulated. Note the medial flare of the trochlea (white line). When the manus is still in stance phase (Fig. 4), the contraction of the elbow extensors imparts parasagittal moments (A) on the olecranon process of the ulna. Flexors with an origin on the medial epicondyle create moments (B) that also extend the elbow, but because their origin is medial to the action of the extensors, a resultant force is a moment rotating the ulna medially (blue), or counter-clockwise and tending to medially translating the ulna. The medial flare typical of monkeys places the joint surface normal to this force and prevents medial dislocation during forceful extension. *Trachypithecus francoisi* specimen from the Human Origins and Primate Evolution Laboratory, Indiana University.

apes. The family Hylobatidae or the lesser apes is made up of two genera: the larger siamang, genus *Symphalangus* (female body mass of 10.7 kg); and the gibbon, genus *Hylobates*, which consists of 13 closely related, allopatric species, all roughly half the size of siamangs (female average 6.1 kg).

The great apes are placed in three genera: *Pongo* (orangutan); *Gorilla*; and *Pan* (chimpanzee). Each genus has two species. The two orangutan species are allopatric; *Pongo abelli* is confined to the island of Sumatra and *P. pygmaeus* is found only on the neighboring island of Borneo. Orangutans and hylobatids are limited to Southeast Asia and both are nearly exclusively arboreal.

The two gorilla species are the western gorillas (*Gorilla gorilla*), which includes the western lowland gorilla and the Cross River gorilla, and the eastern gorilla, *G. beringei*, with mountain and lowland subspecies. The two species are allopatric and quite similar. Both species are highly sexually dimorphic, with males weighing 165.5 kg and females 90.4 kg (body masses from Fleagle, 2013).

The two species of *Pan*, the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) are allopatric and less similar than the two gorilla species. Bonobos are confined to the area inside the big bend of the Congo River in central Africa, while chimpanzees are found only outside the bend and range from west to central to east Africa. Bonobos weigh 45.0 and 33.2 kg, while chimpanzees are slightly heavier at 48.4 and 39.3 kg.

The many anatomical similarities of the apes (to be discussed in detail below) led to the unquestioned assumption through the early 1960s that their shared anatomy was inherited from a common brachiating ancestor. After gibbons and siamangs branched off from the great apes rather early, the great apes continued in a monophyletic clade for a considerable time, only evolving into each of the great ape genera quite late; humans were thought to be a separate clade that branched off before the great apes diversified (Napier & Napier, 1967; Schultz, 1969). A more complete fossil record and the growth of genetic research

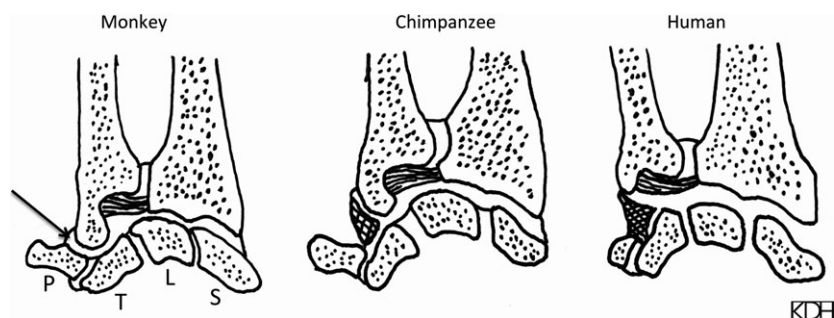


Fig. 6 Wrists of *Cercopithecus* (*C. nictitans*), chimpanzee and human. P, pisiform; T, triquetral; L, lunate; S, scaphoid. In monkeys the ulnar styloid process closely articulates with a cup-like surface formed by the pisiform and triquetral (arrow) stabilizing the wrist but limiting supination. Apes have less tightly articulated carpoulnar articulation, and the styloid process and the carpus have a flexible meniscus between them, allowing ulnar deviation and supination. Humans have an anatomy allowing still more flexibility. After Lewis (1972).

have now made it a settled issue that the first splitting event was the branching of the lesser apes from the great apes at approximately 17 Ma, after which orangutans diverged at ~14 Ma. Gorillas split from the panin/hominin lineage about 8 Ma, and the genus *Pan* diverged from hominins slightly later, perhaps 6 Ma. The final cladogenetic event was the speciation of chimpanzees and bonobos at 2.5 Ma (Raaijmakers et al. 2005; Cartmill & Smith, 2009; Fleagle, 2013).

Gibbons and siamangs

The hylobatids are monogamous and monomorphic; pairs travel together with their dependent offspring and jointly defend a 500-m-diameter territory, which they traverse on a near-daily basis (Carpenter, 1940; Leighton, 1986). Because both sexes engage in territorial defense, neither body size nor canine size differs significantly between the sexes (Plavcan & Van Schaik, 1992). Gibbons are active primates; they move through the forest canopy quickly using a suspensory hand-over-hand locomotion known as brachiation, supplemented with occasional leaping (Fig. 1; Table 3). Hand-over-hand vertical climbing is also part of their repertoire, and as a consequence they have a highly abducted, gripping great toe (Fig. 3). With the exception of sitting, unimanual arm-hanging is their most common posture, a suspensory mode used most often during feeding. The positional profile of the larger siamang (female body mass 10.7 kg) is similar to that of gibbons, although they leap less frequently and vertical climb considerably more often. The siamang positional repertoire is convergent on that of orangutans, presumably as a response to their greater body weight (Collis et al., 1999). Hylobatids engage in bipedalism more than any other primate.

Hylobatids were once considered folivores, but more recent work has made it clear that they resemble other apes in exhibiting a strong preference for succulent ripe fruits. They consume more fruits than sympatric orangutans, macaques and langurs (Ungar, 1995) and fall back on leaves when ripe fruits are unavailable; they supplement their fruit diet with insects (*ibid*).

Orangutans

Orangutans are deliberate, ponderous yet capable arborealists most distinguished from the African apes by their extremely flexible hips (Cant, 1987a; Thorpe & Crompton, 2005, 2006; Thorpe et al. 2007a,b, 2009). During feeding in particular they often engage in hand-foot hanging postures, suspending themselves from ipsilateral fore- and hindlimbs, and a variety of other suspensory postural modes (Cant, 1987a,b; Thorpe & Crompton, 2005, 2006; Thorpe et al. 2007a,b, 2009). Their locomotion is predominantly suspensory, including a high proportion of non-stereotyped locomotor modes wherein the hands and feet bear weight in

tension with the torso held vertical; many similar such behaviors are pooled in the category 'clamber'. Suspensory behaviors such as bridging and transferring are also common (Fig. 1; Table 3; Thorpe & Crompton, 2005, 2006; Thorpe et al. 2007a,b, 2009; Manduelli et al. 2011). They are quite bipedal compared with other great apes (Cant, 1987a,b; Hunt, 1996; Thorpe et al. 2007b), which means that, perhaps unexpectedly, the more arboreal Asian apes exhibit a higher frequency of bipedalism than the more terrestrial African apes (Crompton et al. 2008).

The orangutan social system has been characterized as 'solitary' because individuals frequently travel without other adults. Females confine most of their activities, accompanied by their immature offspring (MacKinnon, 1974; Galdikas, 1984, 1988; Rodman & Mitani, 1986), to undefended core areas that overlap with those of other females and are embedded in a larger male territory. 'Solitary' is somewhat of a misnomer because social groupings are common enough that their society has been described as fission-fusion (van Schaik, 1999; Wich, 2009), or similar to that of chimpanzees. Related females are more likely to establish core areas near one another, more likely to socialize with one another and have more extensive overlap in their core areas (Singleton et al. 2009). Nevertheless, orangutans are distinctly less social than chimpanzees: grooming makes up only 1% of the orangutan activity budget (Fox et al. 2004) vs. 8–12% in chimpanzees (Wrangham, 1977; Nishida, 1990; Boesch & Boesch-Achermann, 2000). Furthermore, the two *Pongo* species differ, Sumatran orangutans having average party sizes of 1.8, vs. 1.2 for Bornean orangutans (van Schaik, 1999; Singleton et al. 2009).

Adult males are found in two morphs, flanged males bearing distinctive fatty pads on their cheeks, and the much smaller, less reproductively successful unflanged morph. The smaller morph is a female-mimic that has evolved a reproductive strategy involving stealth and forced copulation, rather than territorial defense (Utami-Atmoko et al., 2002, 2009; Goossens et al. 2006); small body size may both camouflage unflanged males and afford them greater mobility, thus allowing them to escape quickly when attacked. Flanged males patrol and defend a territory that encompasses the core areas of several females, with whom they form loose bonds. Males announce their presence with a loud call that warns other males, and which females depend on to track their movement. Females move toward territorial males when they enter estrus (Mitani, 1985). Long-calls announce both the current location of territorial males and also telegraph their movements a day in advance (van Schaik et al. 2013).

When males meet, aggression tends to escalate, but encounters are less common than they might be because they alter their daily movements so as to avoid one another. Head-to-head direct competition has selected for great sexual dimorphism with adult flanged males weighing twice what female do, 78.2 vs. 35.7 kg (Tables 1 and 2). The func-

tion of flanges is unexplained, but orangutans lack supraorbital tori, a pronounced ridge of bone that encircles the eyes of African apes, leaving the eyes set deep in the orbit and possibly less susceptible to injury during aggressive encounters. Perhaps flanges serve the same function.

While they are ripe-fruit specialists like other apes (Leighton, 1993; Knott, 1998), orangutans select unripe fruits when they are great enough in number to compensate for the depressed nutrient content characteristic of high-tannin unripe fruits (*ibid*). Orangutans supplement fruits with leaves and to a lesser extent insects and fall back on bark, a critical resource during times of low fruit availability (Leighton, 1993; Ungar, 1995; Knott, 1998).

Gorillas

Gorillas are sympatric with chimpanzees across much of their range and the two species share many food items; the gorilla food species list can overlap with that of chimpanzees up to 100% (Harcourt & Stewart, 2007). Whereas chimpanzees supplement an arboreal diet of ripe fruit with piths and other terrestrial herbaceous vegetation (THV), gorillas rely on THV as a staple, and gorilla population density correlates with the availability of high-quality herbaceous vegetation (Harcourt & Stewart, 2007). While THV is a staple, gorillas still prefer fruit over foliage (Remis, 2002) and preferentially select it when it is abundant (Remis, 1995; Marshall & Wrangham, 2007). Western lowland gorillas include as many as 120 fruit species in their diet, including arboreally harvested fruits that can constitute 35% of their diet (Harcourt & Stewart, 2007). Fruit is a critical enough resource for lowland gorillas that they increase their day range when it is abundant, travelling up to 3 km a day (Harcourt & Stewart, 2007), compared with 0.5 km for mountain gorillas. Gorillas harvest fruits arboreally principally using sitting and squatting postures (~65% of postural bouts). Remis was unable to establish a positional profile that included both terrestrial and arboreal positional behavior (Remis, 1995), and thus gorilla data could not be included directly in analyses here, but it is clear that despite their great body mass they engage in more suspensory behaviors (2%) and other acrobatic postures (Remis, 1995) than had been suspected previously. Mountain gorilla data likewise are not comparable to data presented here (Tuttle & Watts, 1985), but their posture is virtually all sitting or squatting and locomotion is almost entirely knuckle-walking.

The female-choice gorilla social system is one in which multiple (usually unrelated) females are bonded to a single male who guards their offspring against extra-group males and predators (Harcourt et al. 1976; Harcourt, 1978; Fossey, 1984; Stokes et al. 2003; Harcourt & Stewart, 2007; Stoinski et al., 2009). Most females disperse to a new breeding group as they reach maturity and typically disperse again at least once in their lifetime (Harcourt & Stewart, 2007).

Among western gorillas, sisters may transfer to a new group together, in which case kin engage in positive social exchanges (Harcourt & Stewart, 2007) that are unknown among unrelated females, which instead have antagonistic relationships competitive enough that they form dominance hierarchies. Across all habitats breeding group size is rather consistent at eight adults (Harcourt & Stewart, 2007).

The death of the silverback male is the most common motivation for female group transfer; when a female disperses with a nursing infant, infanticide risk is high both before and after she settles with a new male (Harcourt & Stewart, 2007). When breeding groups approach one another, encounters range from unidirectional avoidance by the subordinate group to rather peaceful interactions to lethal violence. Not uncommonly, silverback males engage in flamboyant rushing and chest-beating displays that may segue into physical battles. Some intergroup encounters are initiated by stalker males who track a reproductive group for extended periods before mounting a challenge to the resident silverback. Females are more likely to transfer to a challenger-male's group if he demonstrates superior fighting skills (Stokes et al. 2003). Among mountain gorillas challenges may be deadly; challenger males may kill an infant when he attacks a breeding group, in which case the female whose infant is killed is more likely to transfer to the infanticidal male's one-male unit (Watts, 1989). While intergroup violence or silverback deaths are the most frequent spurs to female dispersal, females may transfer with no discernable signs of the impending dispersal (Harcourt & Stewart, 2007).

Males disperse on reaching adulthood, and may either wander alone or join an all-male bachelor group, some of which persist for years. While 97% of breeding groups contain only one adult male (Harcourt & Stewart, 2007), among mountain gorillas sons remain in their natal group 40% of the time, in which case they mate only with females bonded to them, and their father does the same (Fossey, 1984; Watts, 1991; Robbins, 2001; Yamagiwa et al. 2003). Both father and son defend the social group. As discussed above, this system is a two-male version of the larger multi-level system observed in hamadryas baboons where alliances involve three rather than two males; all three males in the triad cooperate in the mutual defense of their individual one-male units.

Chimpanzees

Chimpanzees are the best-studied of the apes, with wild studies of 55 years or longer at six sites (Wrangham, 1979; Goodall, 1986; Boesch, 1996; Mitani et al. 2002), and briefer but still long-term studies at three times that many. Chimpanzees live in 'closed' groups in which all members recognize one another as constituting a community, also known as a unit-group, while recognizing extragroup individuals as outsiders. A community typically includes a dozen closely

bonded males which, although closely bonded, compete intensely for status and form linear dominance hierarchies; the remainder of the 40 or so community members are females and juveniles (Boesch, 1996). A community occupies an area of approximately 4 km in diameter, wherein males travel widely across the entire community territory while non-estrous females spend two-thirds of their time alone or with dependent offspring in a core area that overlaps with the core areas of neighboring females (Goodall, 1986). Individuals gather in smaller subgroups that are shuffled and regrouped on an hourly basis in what has become known as a fission-fusion social system. Females typically disperse when they reach adulthood, although a substantial number remain in their natal community (Pusey, 1979; Mitani et al. 2002). While the average party size is approximately six individuals (Boesch, 1996), typically consisting of four or five males and one or two estrous females, at times they gather in groups of 20 and more.

Males communally defend a territory against extracommunity males by engaging in aggressive border patrols approximately once a month. Border patrol parties consist mostly of mature males who are seeking an imbalance of power in the form of superiority of numbers. They attack and if possible kill extracommunity males or infants they are unlikely to have fathered; non-estrous females are occasionally killed (Wilson et al. 2014). Such coalitionary violence is extremely rare in the animal world, with only a handful of other mammals exhibiting the behavior (Wrangham, 1999). Chimpanzees engage in physical violence more often than any other mammal, with individuals suffering a physical attack every 44 h (Muller, 2002), and the violence is quite serious. Chimpanzees are perhaps the most murderous of all mammals, and certainly the most murderous of the primates (*ibid*).

Males achieve reproductive benefits through their territorial defense. When territories expand reproductive rates rise and infant mortality decreases (Williams et al. 2004). Furthermore, if all males from a neighboring community are killed, the neighboring territory may be annexed or females may migrate into the territory of the victors (Nishida et al. 1985).

Chimpanzees prefer ripe fruits (Wrangham et al. 1998), but fall back on piths and bark when ripe fruit is unavailable. The sparse and dispersed nature of ripe fruit in comparison to unripe fruit causes chimpanzees to experience food supplies as low (Wrangham, 1977, 1979; Sterck et al. 1997) and precludes female defense of feeding sites. By limiting their ranging to a core area, females can monitor food distribution intensely and harvest preferred food items thoroughly. Because males are dominant and aggressive, they displace females from preferred feeding sites. Larger male body size and freedom from the encumbrance of infant carriage leave them free to form larger groups and to range more widely in their territory. Chimpanzee functional morphology is discussed below.

Bonobos

Bonobos are not sympatric with gorillas, removing a potential competitor for pithy THV and allowing THV to constitute a critical component of their diet (Kano & Mulavva, 1984; White & Wrangham, 1988; Malenky & Wrangham, 1994). The high proportion of THV in their diet is thought to have had profound consequences for their social organization. With a readily available fallback food to sustain large group sizes when ripe fruits are scarce, bonobo party sizes are consistently larger than those of chimpanzees (Badrian & Malenky, 1984; White & Wrangham, 1988; White, 1996). Theoretically, the higher proportion of females in mixed-sex parties allows female bonobos to form alliances and command considerable political power, to the extent that females are typically dominant to males (White, 1996). Females have a prolonged estrus that disguises ovulation, reducing the ability of high-ranking males to monopolize females at the peak of fertility (Kano, 1980; Furuichi, 1992; White, 1996), making male aggression less reproductively advantageous and yielding a considerably less violent society than that of chimpanzees.

Anatomically, bonobos resemble chimpanzees but are less robust, exhibiting less prognathism, a shorter midface, smaller supratatorial sulci, smaller supraorbital tori, smaller brains (Hare et al. 2012) and a more anteriorly placed foramen magnum (Shea, 1984). They have slightly smaller IMIs than chimpanzees, 102 vs. 105. Compared to chimpanzees, bonobo lower limbs, including the feet, are both longer and make up a greater proportion of the body weight, 24% for bonobos vs. 18% for chimpanzees (Zihlman, 1984). Shea (1984) offers a compelling argument that many of these traits are neotenously derived with respect to the common ancestor.

While some have speculated that lower limb features and foramen magnum placement are adaptations to a greater frequency of bipedalism compared with chimpanzees (Susman, 1984; Hohmann & Fruth, 1993), low frequencies of bipedalism in both wild (Susman et al. 1980; Susman, 1984; Doran, 1993) and captive bonobos (Videan & McGrew, 2001) are contrary to this hypothesis. Long hindlimbs and feet might suggest a leaping adaptation, but positional data fail to support this speculation. Note, however, that the positional behavior of bonobos is at present only partly documented. Incompletely habituated bonobos at Lomako bonobos were observed to be more arboreal and more suspensory than chimpanzees (Doran, 1993; Doran & Hunt, 1994), but few terrestrial observations were made and behavior was likely influenced by the lack of habituation. Ramos (2014) has not yet published data on the better-habituated population at Lui Kotale, but preliminary observations suggest that, compared with chimpanzees, bonobos engage in high frequencies of knuckle-walking, spend a considerable proportion of their active period on the ground and only rarely engage in suspensory behavior.

Key issues in ape and cercopithecoid socioecology and ecomorphology

Among the haplorhines it is unusual to find a social system other than female-bonded, a system where related females remain in their natal groups and form close, lifelong bonds (Wrangham, 1980; Sterck et al. 1997). Among the frugivorous Old World monkeys, only populations in harsh, peripheral environments exhibit a non-female-bonded system. Apes, however, are distinguished by their lack of close bonds among related females. Hylobatids, orangutans and gorillas have male–female bonds, chimpanzees have male bonds, and bonobos have mother–son and female non-kin bonds. Orangutans, chimpanzees and bonobos, in particular, live in a ‘virtual’ society where the community is a mental construct wherein each member of the closed social group knows who else is part of the group, but all members of the community are never in one place at one time. Negotiating social challenges in a social environment in which so much social activity occurs off-stage is likely to exert powerful selective pressure on cognition. An entrant into a chimpanzee party may find the subgroup contains individuals who have not been encountered for days during which time alliances may have shifted substantially. It would be advantageous for the newcomer to read the subtle cues that betray such changes quickly and accurately. Monkeys, in contrast, have a socially cohesive system where individuals need not guess at changed relationships; the social group travels together so that every individual sees rank changes, alliance changes and the formation of new relationships as they happen.

Over the last 25 million years, the same ecological forces that drive the unusual, cognitively demanding ape social system have also altered the ape foraging regime, which has in turn driven changes in anatomy. Paleontology can help to determine when ape society shifted from its female-bonded ancestry to their extant non-female-bonded societies by providing information on morphological evolution linked to ecological changes.

Chimpanzee positional behavior

Primatologists have dithered on the issue of whether chimpanzees are best described as terrestrially adapted or arboreally adapted. The ambivalence is inevitable if a dichotomous approach is taken. Chimpanzees are neither terrestrial nor arboreal; they are terrestrial travelers – nearly 99% of their travel is engaged in on the ground – and arboreal feeders; 85% of their feeding behavior is in trees (Hunt, 1989).

Suspensory posture is a vital positional behavior for chimpanzees (Fig. 1; Table 3), but not a common one; it constitutes only 4.4% of all behavior. Unimanual arm-hanging is a feeding behavior: 90% of chimpanzee arm-hanging occurs during food gathering. Arm-hanging is engaged in

to solve a specific challenge; the posture is assumed to enable chimpanzees to negotiate small-diameter, flexible (or compliant) supports found among the outermost branches of the tree canopy. Nearly 80% of arm-hanging is engaged in among the terminal branches, and the smaller the support, the greater the proportion of suspensory behavior. Arm-hanging makes up 2.5% of behavior among supports greater than 10 cm, 8.3% of behavior among 3–10 cm supports, and 24% of behavior when supports are less than 3 cm (Hunt, 1992a).

Suspensory locomotion, likewise, is rare at Gombe and Mahale, and it is engaged in most often among the compliant terminal branches of trees. While suspensory locomotion makes up only 0.2% of all locomotion, its frequency rises to 29.4% in the outermost meter of the tree canopy. Among the smallest category of supports, 8.8% of locomotion is brachiation and 20.6% is orthograde transferring, a mode wherein the individual begins in a suspensory arm-hanging or arm–foot-hanging posture, reaches out to grasp branches in a neighboring tree and transfers weight onto them, thus moving between tree canopies.

An analysis of the impact of social rank on foraging behavior demonstrates that even though chimpanzees are often found in the tree periphery, they prefer to position themselves on larger branches and in the tree core when possible. High-ranking chimpanzees at Gombe and Mahale used larger supports than subordinate individuals, more often sat to feed (Hunt, 1992b), and less often engaged in arm-hanging (Hunt, 1992b). Although high-ranking individuals spent more time in the tree periphery than subordinates, they positioned themselves on larger supports (Hunt, 1992b). Thus, dominant individuals monopolize feeding sites in the terminal branches where ripe fruits are most often found, but they access food using a stable, presumably less fatiguing, sitting posture possible on the larger supports they monopolize (*ibid*). Low-ranking individuals have less access to the ripe-fruit-rich terminal branches, but at the same time they are compelled to feed among smaller, less stable supports (*ibid*). This contrast is important; even within 1 m of the canopy edge there are some feeding sites with large, stable supports even though most feeding sites are among small-diameter, precarious supports. The diameter of supports is only critical because small-diameter branches tend to be more compliant; flexibility is the critical feature, not diameter alone (Thorpe et al. 2007b).

In other words, chimpanzees engage in suspensory behaviors such as arm-hanging and brachiation not because it is a preferred positional mode, but because it is the most effective means of negotiating small-diameter, flexible supports in the tree periphery, where the ripe fruit is.

The rarity and dispersed nature of the preferred chimpanzee food, ripe fruit (Wrangham et al. 1998), affects travel choices. When an adjacent tree offers edible foods, which is uncommon, chimpanzees move between tree

crowns by suspensory transferring, brachiation or (rarely) leaping. A long feeding bout is more often followed by hand-over-hand vertical descension or arboreal walking, perhaps ending with a bimanual suspensory drop. That is, in the lower strata of the tree canopy individuals may palm-walk along a horizontal branch, moving toward the tree periphery, causing the support to bend under the individual's weight; he or she might then grasp the branch with two hands, suspend bimanually underneath it and drop the final few meters to the ground. Occasionally, after swinging under the branch, an individual might brachiate along the length of it before dropping, though rarely more than two or three strides.

Descension is sometimes followed by a short locomotor bout ending at a desired socializing location, a spot surprisingly often found in the midst of a vine tangle, after which individuals may groom or rest quietly, sitting or lying on the ground. More often, individuals knuckle-walk immediately to the next feeding tree and enter it by vertical climbing. It is apparent that vertical climbing is fatiguing from the observation that the positional mode that most often follows vertical climbing is sitting, while the most common contexts following climbing are resting and grooming (Hunt, 1989). After a brief rest on a large branch, a forager might then knuckle-walk and (as smaller supports are encountered) palm-walk to the tree periphery where harvesting might occur with a sitting posture, if the support is large enough, or arm-hanging if the support is small-diameter and compliant.

The most frequently observed positional mode among chimpanzees is sitting (Fig. 1; Table 3) but, when they are in a comfortable perch, they often lie. Terrestrial knuckle-walking makes up a large part of the active period, over 15%. Chimpanzees travel ~5 km a day at a slow pace, two–three times slower than expected for their body mass (Hunt, 1989; Pontzer & Wrangham, 2004); when they are unhurried their pace may be slow enough to be somewhat uncomfortable for a human observer. Long uninterrupted walking bouts that are perfectly comfortable for a human may leave chimpanzees visibly fatigued and they may pause to rest until their respiration rates return to normal (personal observation).

In the tree canopy chimpanzees typically ascend and descend with a hand-over-hand vertical climbing locomotion. Knuckle-walking is a rare arboreal behavior, making up only 6.3% of all arboreal locomotion (Hunt, 1992a; Table 7); it is uncommon in trees because it is practical only on very large supports (≥ 10 cm). As support diameters decrease, chimpanzees switch from knuckle-walking to palm-walking (Hunt, 1992a), a mode wherein the wrist is supinated so that the long axis of the manus is nearly perpendicular to the support; the manus is dorsiflexed and weight is borne on the palm just distal to the base of the thumb or on the thenar pad. The fingers are little-used for gripping in this mode and the thumb, so far as observed by the author, is

almost never recruited. Dorsiflexion in this supinated position is somewhat unexpected because chimpanzees have little dorsiflexion in pronation (Tuttle, 1969, 1970). This mode may be responsible for some of the unusual and as yet unexplained morphology of the chimpanzee carpus.

Feeding bouts begin most often after an individual ascends a rather small-diameter, near-vertical support using a vertical climbing mode. While vertical climbing on large-diameter boles (e.g. > 20 cm) may be a critical behavior when no other access to a particular tree is possible, chimpanzees consistently select small-diameter supports such as a sapling, smaller tree or liana for ascents. At Gombe and Mahale, fully 50% of vertical climbing utilized supports 4 cm or smaller, and only 5% of vertical climbing was engaged in on boles 20 cm or larger (Hunt, 1992a). It is suspected that chimpanzees pass over trees that can be accessed only via a large bole. Some trees that have no small-support access may be reached by transferring, scrambling or leaping from an adjacent crown.

Chimpanzee positional behavior contrasted to that of monkeys

A comparison of chimpanzee positional behavior to that of similar-sized baboons (*Papio anubis*) occupying the same ranges and in many cases foraging in the same trees (Fig. 1; Table 3; Hunt, 1992a) suggests that two chimpanzee positional modes are distinctive and therefore responsible for distinct chimpanzee anatomy: unimanual suspension (arm-hanging: 4.4% of all behavior vs. 0% for baboons) and vertical climbing (0.9% vs. 0.5% for baboons). Baboons engage in four modes significantly more often than chimpanzees: walking (23.2% : 16.3%); leaping (0.2% : 0%); standing (14.5% : 2.5%); and (to a lesser extent) running (Table 3). Differences between the two species are most striking in the contexts of feeding and ascents/descents.

Monkeys and apes take different approaches to ascension of the same tree. One incident (personal observation, Gombe, November, 1986) demonstrates this difference; a chimpanzee entered a tree crown by vertical climbing an approximately 15 cm vertical bole, but climbed only for 2 m to reach the first horizontal branch. It then vertical climbed further not by gripping a vertical bole, but by grasping horizontal branches near the bole and ascending in a manner similar to a human climbing a ladder. A male baboon ascended the same tree moments later by making a prodigious leap to the first horizontal branch, then leapt branch to branch in a spiral path around the bole, ascending to the same elevation as the chimpanzee. Climbing is less important for monkeys because they travel arboreally more often, obviating the need for ascents and descents. Rather than descending to the forest floor to travel, as chimpanzees do, monkeys typically leap between tree crowns and walk quadrupedally within the crown to their next feeding site (Table 1).

In comparison to chimpanzees, antifeedant-tolerant monkeys experience the forest as more bountiful. With a diet higher in unripe fruits and the ability to consume a wider variety of leaves, blossoms, shoots and buds, monkey food resources are experienced as more abundant and less dispersed (Wrangham et al. 1998), allowing monkeys to feed more often in the tree core where their smaller body size and the availability of larger supports allows them to feed while sitting (Hunt, 1992a). Monkeys possess fibrous ischial sitting pads or ischial callosities as adaptations to prolonged sitting, which they engage in during sleeping as well as feeding (Washburn, 1950, 1957). Whereas all baboons have ischial callosities, only 36% of chimpanzees do (Schultz, 1936, 1940). Chimpanzees and baboons sit equally often (Hunt, 1992a) during daylight hours, supporting the contention that ischial callosities are a sleeping adaptation (Washburn, 1957). If so, the persistence of callosities in chimpanzees suggests that sleeping platforms, and perhaps associated cognitive advances (Samson & Shumaker, 2013; Samson & Hunt, 2014; Samson & Nunn, 2015), may have appeared late in chimpanzee evolution.

While it is clear that the capacity to engage in suspensory behavior is an adaptation that functions to allow access to compliant, small-diameter supports in the tree periphery (see above), there is no definitive resolution to the issue of whether chimpanzees and other apes have evolved suspensory behavior to gain 'better' access to terminal branches, or to keep access to such feeding sites 'equivalent' to that of monkeys, despite larger ape body size. Most studies examining the use of support diameters either surveyed monkeys but not apes (Fleagle, 1976a, 1977, 1978; Gebo & Chapman, 1995; McGraw, 1998a,b; Houle et al. 2006), or apes but not monkeys (Doran & Fleagle, 1976b; Cant, 1987a,b; Sugardjito, 1982; Thorpe & Crompton, 2005, 2006; Thorpe et al. 2007a; Manduell et al. 2011). Cant (1992), however, compared two apes with two monkeys; he found that macaques feed in middle and lower canopy strata, langurs and orangutans use all levels, and gibbons focus on middle and upper levels, but he did not provide support diameters. Cannon & Leighton (1994) found that during gap-crossings gibbons could negotiate the small-diameter branches in the tree periphery better than the similar-sized macaque.

Related to the capacity of different species to negotiate small supports is the issue of the exact location in the canopy of ripe fruits, the foods apes depend upon. Recently, Houle and colleagues (Houle et al. 2006, 2007, 2010, 2014) showed that the upper half of trees produce nearly five times the density of fruits, produce larger fruits, bear at any one time riper fruits, and contain fruits with higher concentrations of sugars and fewer toxins. When chimpanzees feed in the same trees as redbell monkeys, blue monkeys and mangabeys, chimpanzees monopolize the higher, more productive portion of the tree canopy, dis-

placing monkeys to lower feeding sites with unripe fruits (Houle et al. 2010). These results elegantly interdigitate with Cant's (1992) findings, assuming that it is the folivorous diets of langurs that allow them to overlap with orangutans. Cannon and Leighton's results support the contention that apes evolved larger body size as a response to contest competition, and that monkeys responded by evolving a tolerance for antifeedants. In such a scenario, suspensory behavior may have evolved to afford chimpanzees and other apes with 'equal' access to resources that their larger body mass might otherwise make inaccessible to them, while monkeys may have evolved antifeedant-tolerant digestive physiology as a scramble competition response to displacement from preferred feeding sites. Monkeys, by retaining or evolving small body sizes, are superior scramble competitors because they can utilize small, low-density fruit crops that are below an ape's 'giving-up' density (Brown, 1988, 1989; Brown et al. 1994), and because small size affords them equal or better access to small branches. The two hypotheses—(i) apes have evolved better access to terminal branches in order to harvest the only ripe fruits available to them after monkeys have had earlier access; and (ii) apes compete by excluding monkeys when both taxa feed at the same time, and apes have suspensory capabilities to maintain equal access—are eminently testable. In the scenario judged more likely here, chimpanzees compared with monkeys are expected to arrive at individual trees later in the fruiting cycle on average, and chimpanzees are expected to feed on average closer to the canopy edge (i.e. peripheral terminal branches). In the 'giving-up-density' alternative, no difference in the timing of the arrival of monkeys and chimpanzees at individual trees is expected, there should be no difference in the proximity of monkeys and chimpanzees to the tree edge or in branch sizes, and when feeding from the same trees monkeys should remain in trees longer. Both scenarios are consistent with the hypothesis that suspensory behavior evolved as an adaptation for harvesting fruits among compliant, peripheral branches, and that apes evolved larger body size in part to displace monkeys, while monkeys evolved antifeedant tolerance to compete with apes.

Kinematics, joint excursions and loose ends

Distinguishing the differing skeletal and muscular correlates of vertical climbing vs. the correlates of unimanual arm-hanging and other suspensory behaviors is critical for interpreting chimpanzee and monkey functional morphology, which is in turn essential for reconstructing the ecomorphology of fossil species. Complete separation is not possible, because the demands made on specific anatomical structures can be nearly identical for different positional modes; for example, strong gripping of cylindrical supports is required for suspensory posture, suspensory locomotion and vertical climbing. While complete disentanglement is

impossible, better resolution than we currently possess is possible.

Fleagle and colleagues (Fleagle et al. 1981; see also Stern et al. 1977; Prost, 1980) argued that anatomical features that allow full forelimb abduction, full elbow extension and that require the body weight to be borne by a single manus/forelimb are adaptations to vertical climbing rather than suspensory behaviors, arguing that when reaching up for a higher handhold the shoulder is fully abducted. Hunt and colleagues (Hunt, 1991, 1996) and others (Larson, 1998; Fleagle, 2013) argued that these features were principally adaptations to unimanual arm-hanging and/or suspensory locomotor adaptations because vertical climbing in wild chimpanzees involves full abduction and full elbow extension only rarely (Hunt, 1991).

Following Fleagle et al. (1981), Doran (1993, 1996) found support for the hypothesis that vertical climbing is responsible for ape shoulder mobility and full elbow extension. Her observations of chimpanzees at Tai, Ivory Coast indicate high frequencies of climbing and low frequencies of unimanual arm-hanging (1.3% of all behavior). She concluded that arm-hanging is not common enough to require substantial adaptations, and that the more frequently observed climbing is the most distinctive chimpanzee positional mode. Two lines of reasoning argue against this interpretation and support the suspensory hypothesis. First, a frequency of 1.3% for arm-hanging is high compared with the frequency of 0.0% among African cercopithecoids (Fig. 1; Table 3), and it is greater than Hunt's figure for vertical climbing (0.9%, Hunt, 1991). Second, Doran's protocol did not distinguish between vertical climbing and suspensory and walking modes, but instead (Doran, 1989, p. 328) utilized the catch-all category 'climbing' for a rather broad swath of arboreal behaviors, some of which required both a fully extended elbow and a fully abducted humerus others of which did not. Her category 'climbing' pooled vertical climbing with the suspensory modes quadrumanous climbing, clambering, bridging and tree swaying, and with the quadrupedal modes 'walking on inclined boughs' and scrambling (erratic pronograde quadrupedalism typically engaged in on smaller supports). This pooling exaggerates the frequency of climbing and at the same time decreases the values for suspensory modes by pooling them with climbing modes. Contributing to the confusion is the tendency of functional anatomists to interpret 'climbing' as meaning 'vertical climbing' when making functional arguments.

Isler (2005) supported the vertical-climbing-is-linked-to-elbow-extension-and-shoulder-mobility hypothesis from a different perspective. She analyzed 3D kinematics during vertical climbing and demonstrated that three species of ape, orangutans, gorillas and gibbons, often fully abduct their forelimbs during vertical climbing. One drawback to her study is that she observed her captive experimental subjects as they locomoted on a rope, a support unlike

any a wild ape might climb. Vertical climbing in the wild is engaged in on stiffer and often quite rigid supports, allowing the torso to be tilted away from the vertical support to increase friction on the pes (Jungers, 1976; Sarmiento, 1987, 1989). The leaning-back kinematic during rigid-support vertical climbing closes the angle the humerus makes with the thorax, precluding the need for full abduction. Vertical climbing on non-compliant supports involves a relatively short stride, which further decreases the need for full abduction. Experiments on apes ascending non-compliant substrates will resolve this issue: if the elbow is fully extended and the arm fully abducted during vertical climbing on supports that simulate those in the wild, then a reduced olecranon process and a fully abductible forelimb may well be at least in part adaptations to vertical climbing. If not, not. The high frequency of vertical climbing in colobines and cercopithecines (Fig. 1; Table 3), which lack these two features, is more consistent with the arm-hanging rather than vertical climbing hypothesis.

Clearly the issue is not resolved; however, most interpretations of ape functional anatomy consider suspensory behavior (though not always unimanual arm-hanging) as the principal positional mode for which full abduction, full elbow extension, long ventrally curved digits and certain other ape specializations are evolved (Chivers, 1972; Andrews & Groves, 1976; Fleagle, 1976b, 2013; Sabater Pi, 1979; Susman et al. 1980; Sugardjito, 1982; Fleagle & Kay, 1983; Gittins, 1983; Hollihn, 1984; Kano & Mulavwa, 1984; Srikosamatara, 1984; Susman, 1984; Sugardjito & van Hooff, 1986; Cant, 1987a,b).

Other ape specializations are less controversial. As discussed below it is generally accepted that an abducted great toe with the capability of powerful gripping and muscular specializations related to forceful arm lowering are adaptations to vertical climbing (Table 6; Tuttle & Basmajian, 1977, 1978a; Hollihn, 1984; Preuschoft & Demes, 1984; Thorpe et al. 1999). Still, the issue is not without its loose ends because other ape features such as long arms may well be adaptations to both climbing and arm-hanging (see below).

The distinction between the vertical climbing and arm-hanging hypotheses is not trivial. Hunt (1998) has argued that australopiths exhibit a great number of anatomical features linked to arm-hanging (e.g. cranially oriented scapular glenoid, narrow scapula, robust palmarly curved rays, presence of flexor sheath ridges, perforated olecranon process and cone-shaped thorax), but few or no features linked to vertical climbing (they retain a long lumbar vertebral segment, have short ilia and lack a grasping great toe). Short but otherwise ape-like manual digits suggest australopiths were adapted to grasping branches smaller and more compliant than those typically grasped by apes; such supports are the only ones available in short-statured, small-canopied dry-habitat trees (Hunt, 1994, 1998).

Chimpanzee functional anatomy

Osteoligamentous adaptations

Chimpanzees share a number of anatomical specializations with other apes: long forelimbs with especially long brachii (yielding a high brachial index), long palmarly curved manual rays, short hindlimbs, craniolaterally oriented scapular glenoid fossae, small olecranon processes, mobile shoulders, broad femoral condyles, robust, highly abductible gripping great toes, taillessness, and distinctively wide, shallow thoraxes (Fig. 7) and resultant prominent shoulders (Keith, 1891, 1923; Schultz, 1930, 1936, 1953, 1963; Washburn, 1950; Erikson, 1963; Tuttle, 1970; Rose, 1988a,b).

Whereas other apes are relatively more completely adapted to either terrestrial [mountain (but not lowland) gorillas; Sarmiento, 1994] or arboreal travel (gibbons, siamangs, orangutans), chimpanzees and presumably bonobos are adapted to both. Rose (1991) was the first to emphasize that chimpanzees in particular have a 'compromise' anatomy that can be neither fully adapted to the demands of arboreal positional behavior nor to terrestrial knuckle-walking. Chimpanzee terrestrial locomotion is inefficient (Taylor & Rowntree, 1973), reflecting compromises to joint stability and efficiency required to maintain arboreal competence. In support of this perspective, Pontzer & Wrangham (2004) showed that in their daily activities chimpanzees expend 10 times as many calories walking as vertical climbing. They conclude that walking inefficiency among chimpanzees is compelling evidence that arboreal behaviors are vital to chimpanzee survival. These conclusions are in accord with

data that show that chimpanzees harvest the overwhelming majority of their food in trees (Hunt, 1989, 1991, 1992a).

There are two non-mutually-exclusive hypotheses for the selective value of long forelimbs and high IMIs (IMI = percentage of forelimb length relative to hindlimb length), and there is no consensus as to which selection is primary. Long arms have been hypothesized to increase foraging efficiency by increasing the diameter of the 'collecting sphere', an imaginary volume defined by forelimb length and shoulder mobility in which food items can be collected (Tuttle, 1969; Grand, 1972). A large-diameter feeding sphere hypothetically allows more food items to be gathered from a single perch, improving efficiency by reducing the number of feeding-site shifts required during a feeding bout and thus reducing locomotor costs (Tuttle, 1969; Grand, 1972). Long arms also allow apes to reach into the terminal branches to gather food while their center of gravity remains on more stable supports nearer the tree core (Tuttle, 1969). Greater reach also increases the number of supports available from a given perch (Grand, 1972). The hypothesis that heavier primates require greater reach to access small branches is in accord with evidence that forelimb length scales with body weight (Jungers, 1985; Cant, 1987a). Evidence that dominant male chimpanzees utilize larger supports during feeding, even after adjusting for body size differences, supports the concept that access to large supports near the tree periphery is a priority when such supports provide equal access to ripe fruits (Hunt, 1992b). Reducing postural shifts by utilizing greater reach is also advantageous because terminal branch feeding sites likely offer few useable supports, and increasing the collecting sphere allows individuals to reach more food items from

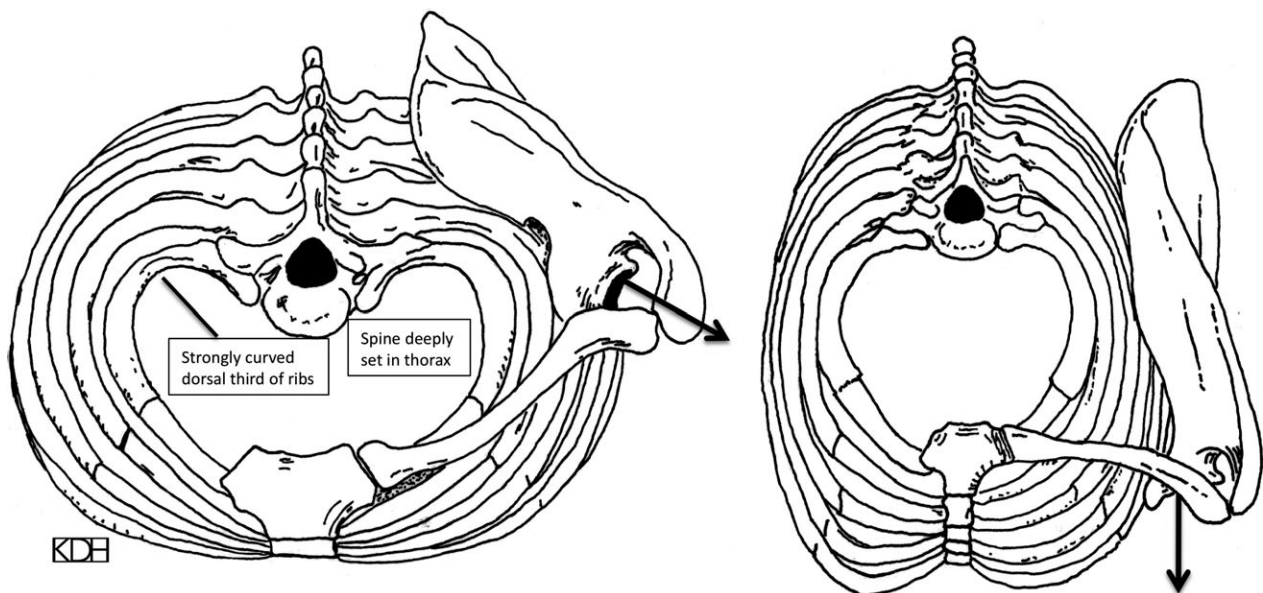


Fig. 7 Cranial views of the thorax of a hominoid (left) and cercopithecoid (right). The ape and human thorax is broad and shallow (top to bottom dimension here), whereas the monkey thorax is narrow and deep. The glenoid fossa (arrow) is oriented laterally and superiorly in hominoids, ventrally in monkeys. The hominoid clavicle is long, the manubrium is wide and the vertebral column is deeply set in the thorax. After Schultz (1950).

one position. The long-reach hypothesis views short hindlimbs as adapted to lowering the center of gravity and thus improving stability and maneuverability on unstable or compliant supports (Jungers, 1984). Thus, this hypothesis holds that the high IMI of apes is a consequence of selection for long forelimbs for feeding and short hindlimbs for better arboreal balance.

This hypothesis is supported by muscle architecture [physiological cross-sectional area (PCSA); Payne et al. 2005, 2006] and electromyogram (EMG) data. Digital flexors are virtually the only active muscles during arm-hanging, implying extensive skeletal and ligamentous adaptations to assure that body weight is borne by skeleton, ligaments, intramuscular septa and/or passive muscular tension during suspensory behavior (see below for more thorough discussion; Table 5; Tuttle & Basmajian, 1974, 1977, 1978a,b; Tuttle et al. 1983; Preuschoft & Demes, 1984). The erratic angulation and unpredictable placement of branches requires orientation of limbs in a wide array of angles requiring that terminal branch foragers have large joint excursions. Chimpanzee muscle architecture (PCSA; Payne et al. 2005, 2006) allows a great range of motion and the maintenance of great power through a wide range of motion (Thorpe et al. 1999), as is necessary among erratically placed supports.

An alternative hypothesis is that long arms and short legs increase friction on vertical supports that are too large to grip with the pes, allowing apes to ascend larger boles than monkeys (Kortlandt, 1968, 1974; Cartmill, 1972, 1974; Jungers, 1976; Mendel, 1976; Stern et al. 1977; Jungers & Stern, 1980, 1981, 1984; Jungers & Susman, 1984; Sarmiento, 1987, 1989). While vertical climbing is uncommon on such large boles (Hunt, 1992a), chimpanzees and orangutans do occasionally climb large tree trunks using an 'extended-elbow' locomotor mode (Hunt, 1992a; Isler & Thorpe, 2003) and they do so capably, quickly and gracefully, suggesting that they have evolved adaptations to this mode. Some argue that high IMIs improve vertical climbing competence even on smaller supports (Cartmill, 1974; Jungers, 1976; Sarmiento, 1985). The high brachial index of hominoids is less controversial and seems best explained as an adaptation to the long-reach hypothesis, but may be a pleiotrophic effect of selection for long fingers, which are in turn more likely to be adaptations for arm-hanging than vertical climbing.

Positional behavior data argue against the hypothesis that long arms are an adaptation to vertical climbing alone, one prediction of which is that in a comparison of multiple species, high frequencies of vertical climbing should accompany long arms. Instead, colobines and arboreal cercopithecines exhibit higher frequencies of vertical climbing than apes (Fig. 1; Tables 2 and 3), yet the IMIs of arboreal cercopithecines and colobines are 81.4 and 87.0, respectively, vs. 130 for the similar-sized gibbon. This comparison, however, is inconclusive because in practice it is often the case that walking on inclined boughs and other behaviors dissimilar to vertical climbing (*sensu stricto*) have been pooled with climbing.

Further arguing against the vertical climbing origin for high IMIs is evidence that among sympatric chimpanzees and olive baboons there was no difference in bole diameter during vertical climbing (Hunt, 1992a).

It seems most likely that the need to engage in both behaviors has selected for long forelimbs. Indeed, despite occasional single reports in support of one or the other of the climbing and suspensory hypotheses, taken as a whole body of work many scholars seem to support this dual-origin hypothesis (Sarmiento, 1983; Fleagle, 2013).

Ape metacarpals and manual phalanges are long (with the exception of gorillas), robust, dense and ventrally curved. Phalanges have pronounced, robust flexor sheath ridges to anchor the flexor tendons, thus preventing bowstringing, features that are generally agreed to be adaptations to suspensory behavior (Tuttle, 1969). Chimpanzee and orangutan phalanges and metacarpals are disproportionately long even in relation to their elongated forelimb (Schultz, 1930, 1936; Figs 15 and 16). Such elongation suggests that some positive selective force maintains digit length in particular rather than that long digits are merely a consequence of selection for a long forelimb. Long fingers allow apes to circumduct larger supports (Cartmill & Milton, 1977; Preuschoft & Demes, 1984; Hunt, 1991), a necessity for suspensory behavior but not for most other modes where the limbs are in compression. Ray curvature in the apes parallels the degree of arboreality and in particular the frequency of suspensory activity (Susman, 1979; Hunt, 1991). Curvature serves a muscle-sparing function during suspensory behavior (Sarmiento, 1988), reduces bending strains on digits when tightly gripping a cylindrical object (Preuschoft et al. 1993) and distributes force more evenly around the circumference of vertical support, thus reducing tissue strain at highly compressed hot spots (Hunt, 1991).

Knuckle-walking, bearing weight on the dorsal aspect of the second manual phalanges with the fingers flexed but the first phalanx hyperextended against the metacarpal heads, is a manual positioning unique to the African apes. As an adaptation to stabilize the phalanges against the metacarpals, the dorsal surface of the distal metacarpals has a distinct mediolaterally oriented ridge just proximal to the metacarpophalangeal articular surface that serves to limit phalangeal dorsiflexion (Tuttle, 1969, 1970, 1975). Whereas dorsal ridges are found in some larger terrestrial monkeys, the ridges are quite pronounced in knuckle-walkers and thus likely an adaptation to knuckle-walking. Other hypothesized adaptations to knuckle-walking such as a beaked scaphoid, dorsal concavity of the scaphoid, waisting of the capitate, distal concavities on the hamate and capitates, and dorsal ridges on the hamate and capitate (Tuttle, 1969, 1970, 1975) have been argued recently to be much more variable among the African apes than previously appreciated and are as often seen among orangutans as knuckle-walkers (Dainton & Macho, 1999; Inouye & Shea, 2004; Kivell et al. 2009).

Table 5 Distinctive chimpanzee traits and their likely function.

Feature	Function	Positional mode implicated
Long arms	Increase foraging reach or increase friction on sole	AH, VC
Long fingers	Circumduct support during suspension	AH
Robust manual digits	Resist bending stresses	AH
Large flexor sheath ridges	Anchor powerful digital flexors	AH
Curved phalanges	Decrease stress on fingers, better circumduct support	AH
Small thumbs	Improved high-velocity grasping ability	LE, SL
Dorsal ridges	Prevent hyperextension of the manual phalanges	QKW
Reduced ulnar styloid, distal pisiform	Allow wrist rotation, ulnar deviation	SL, AH
Bowed radius, ulna	Increase moment arm for pronation, supination	AH
Circular radial head	Allows rotatory wrists	SL, AH
High brachial index	Increases foraging reach	AH
Large supinators and pronators	Adjust position during feeding	AH
Reduced olecranon process of ulna	Allows full extension of elbow	AH, SL
Deep or perforated olecranon fossa	Allows bony support of elbow joint during suspension	AH
'Wrap around' trochlear surface	Allows full extension of elbow	AH
Spool-shaped trochlea	Elbow stability; powerful flexion during suspension, climbing	AH, VC
Prominent coronoid process	Allows elbow flexion from full extension	AH, (SL)
Distally displaced humeral tubercles	Allows shoulder mobility	AH
Extended acromion process	Longer lever arm for biceps	AH
Extended coracoid process	Longer lever arm for biceps	VC
Globular, expanded humeral head	Allows shoulder mobility, weight-bearing	AH, SL, WA
Narrow bicipital groove	Allows shoulder mobility	AH, SL
Broad, ovate glenoid	Prevent dislocation when limb position is erratic	SC, SL
Cranially oriented glenoid	Reduce stress on GHJC	AH, SL
Large conoid ligament	Bears body weight during suspension	AH
Coraco-acromial ligament	Resist cranial dislocation of humerus	AH, SL
Broad manubrium, sternum, fused sternbrae	Bear forces during arm-hanging, arm-raising	AH
Dorsoventrally shallow, broad ribcage	Reduce dorsoventral compression, rib-bending, increase excursion of humerus	AH
Sharply curved ribs	Reduce dorsoventral compression of the thorax	AH
Long clavicle	Consequence of the broad thorax	AH
Cone-shaped ribcage	Reduce compressive mediolateral stress upper thorax	AH
Narrow scapula	Reduce stress on thorax, GHJC	AH
Long scapula	Increase lever arm for serratus	AH, VC
Low humeral torsion	Consequence of broad torso	AH
Short lumbar vertebra segment	Resist buckling forces	VC
Short, broad lumbar vertebrae	Resist buckling forces	VC
Tall pelvis	Resist buckling forces	VC
Broad pelvis	Maintain hip extension in face of great body mass	VC
Large femoral head	Allows eccentric hip movement	SL, NST
High femoral neck-shaft angle	Allows greater hip mobility	NST, TR
Broad femoral condyles	Resist mediolateral moments large due to broad thorax	AH
Robust, gripping great toe	Propel body weight upward during vertical climbing	VC
Long, curved toes, digits II–IV	Allows gripping large vertical supports	VC
No tail	Large body size? Terrestrial ancestry?	?
Lg biceps, brachialis, brachioradialis	Elbow flexion	VC
Large latissimu dorsi, post. Deltoid	Humeral retraction	VC
Robust flexors	Strong manual gripping	AH/SL
Arm flexors, abductors	Arm raising	VC, AH
Large body mass	Defend fruit, process piths and herbs	
Thin enamel, Y-5	Ripe fruit diet with foliage fallback	
Large incisors	Piths, herbs and large fruit processing	

Parentheses: secondary adaptation; AH, arm-hanging; GHJC, glenohumeral joint capsule; LE, leaping; NST, non-stereotyped posture or locomotion requiring eccentric joint excursions; QKW, quadrupedal knuckle-walking; SC, scrambling; SL, suspensory locomotion such as transferring, brachiation or (for orangutans) clambering; TR, orthograde suspensory movement among small-diameter supports and when transferring between tree crowns; VC, vertical climbing; WA, either QKW or palm-walking.

Although there is less hard evidence to support the argument than might be desired, it seems extremely likely that the knuckling hand positioning of African apes is an adaptation to long-distance terrestrial walking, one that reduces the disadvantages extremely long fingers impose on walking. Long fingers create prohibitively large bending moments on the various manual joints during palmigrade progression. When hand placement involves uneven surfaces, particularly if the raised surface is high at the point of contact of the fingers and low at the point of contact of the palm, hyperextension results, bending moments at the joints are high and there is a danger of dislocation. Rapid locomotion both creates larger moments and at the same time reduces the ability to inspect support surface for unevenness. The disadvantages of long fingers are exaggerated by curved phalanges (Tuttle, 1969, 1970) because they rotate the joint surfaces of the digits palmarly, requiring hyperextension merely to place the manus on a flat surface. Flexing the fingers in a knuckling position accommodates the inconvenient orientation of the joints in a primate with strongly ventrally curved phalanges and presents a much smaller footprint to the substrate, thus allowing African apes to mimic the small contact area of cursors while at the same time reducing moments at the carpophalangeal joint. We might expect to find in the fossil record that long-distance travel, long manual rays and ventrally curved phalanges are a co-evolved functional complex, and that knuckle-walking evolved to accommodate long distance travel in primates that were also suspensory.

Reduced articulation between the ulnar styloid process and the carpus, distal displacement of the pisiform removing it from articulation with the ulna (Figs 6 and 9; Table 5; Cartmill & Milton, 1977) and a neomorphic diarthrosis between the radius and the ulna (Midlo, 1934; Lewis, 1965, 1971) compared with Old World monkeys (Benton, 1967; Jones, 1967; Jenkins, 1973; O'Connor, 1975, 1976; Sarmiento, 1988, 2000) allow extensive ulnar deviation and pronation/supination in apes, as well as general wrist mobility, a feature also found in lorises (Cartmill & Milton, 1977). Flexible wrists and mobile shoulders allow suspensory locomotion among erratically angled supports, positional modes such as scrambling, palm-walking (both thorax-pronograde modes), brachiation, transferring and other orthograde suspensory behaviors. Hunt (1991, 1992a) suggested that long fingers and a reduced articulation between the carpus and ulna, thus allowing greater ulnar deviation (Tuttle, 1965, 1969; Jenkins & Fleagle, 1975; Sarmiento, 1988, 2000), are also an adaptation to reduce stresses on the wrist when arm-hanging among vertical supports. Gripping a vertical support requires ulnar deviation of the manus; the longer the fingers, the less ulnar deviation is required. During arm-hanging, 19% of supports were within 30° of true vertical (Hunt, 1991; Table 3).

Chimpanzees have a strongly bowed radius and ulna (Fig. 8; Lewis, 1969; Sarmiento, 1985, 1987, 1988; Rose,

1988b; Rose et al. 1992; Stern & Larson, 2001; Crompton et al. 2008), and powerful supinator, pronator teres and pronator quadratus muscles (Fig. 8; Table 5; Oxnard, 1963; Lewis, 1969; Stern & Larson, 2001). The large PCSA of these muscles and the larger moment arms of the bowed radius and ulna allow chimpanzees to rotate their wrists with great power. A more medially positioned radial tuberosity increases the mechanical advantage of the biceps brachii as a supinator (Aiello & Dean, 1990). Powerful supination and pronation are required during arm-hanging when individuals maneuver among inconveniently placed, erratically ori-

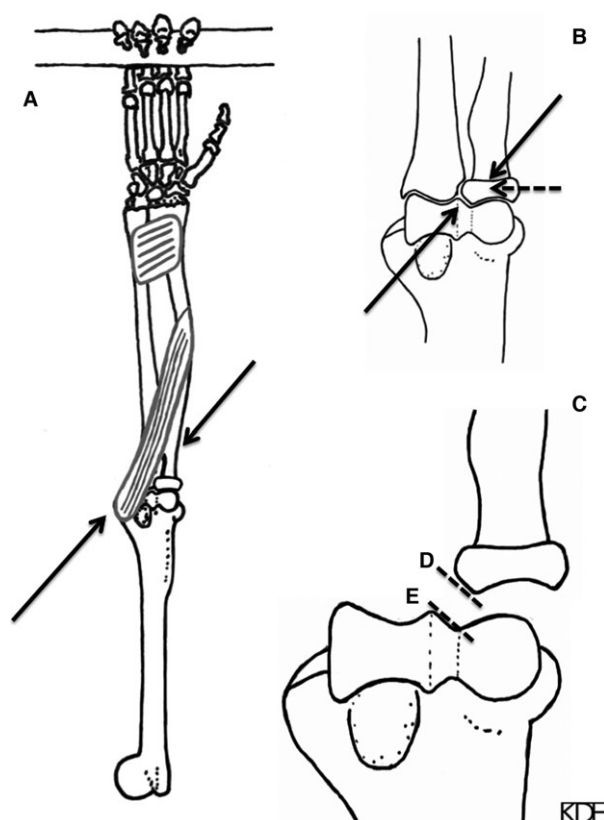


Fig. 8 Ventral view of the right forelimb of a chimpanzee in an arm-hanging posture (A). Close-up of forces acting on the radial head during arm-hanging (B), and view of the articular surface of the radial head and its complementary articulation on the zona conoidea of the humerus (C). During arm-hanging (A), posture is constantly adjusted by contractions of pronator teres and pronator quadratus (gray) to apply torque to the supporting branch (Stern & Larson, 2001) as the need to rotate the body arises. Supinators rotate the body in the opposite direction. Contractions of the pronators create proximal and medial forces on the radial head (B), creating a medial component of the force (dotted line) that tends to medially dislocate the radial head. When the pronators contract, the partly proximal/distal orientation of pronator teres (A, lower gray muscle) presses the beveled articulation of the radial head (C, dotted line D) against the steeply angled zona conoidea of the humerus (E). The combination of the angled orientation of pronator teres, the beveled articulation of the radial head (D) and the angled zona conoidea (E) prevent lateral dislocation of the radial head. After Ziegler (1964) and specimens in the Human Origins and Primate Evolution Laboratory, Indiana University.

ented supports, often rotating the wrist against the fixed upper support (Tuttle et al. 1972; Stern & Larson, 2001) to rotate the body; such behaviors occur often during feeding as the individual depletes food items at one site and pivots toward another. It is sometimes assumed that postures such as arm-hanging involve little movement (Young, 2003), but repositioning by rotating the thorax against the manus, subtle shifts in posture and switching weight-bearing cheiridia can involve considerable muscular effort (Stern & Larson, 2001), and these movements are engaged in on a second-by-second basis during feeding (personal observation). Stern & Larson (2001) contend that adaptations for powerful pronation/supination evolved for positioning the body during this sort of arm-hanging. The contraction of the pronators and supinators during arm-hanging tend to medially displace the radial head; apes have evolved a beveled radial head and steeply angled zona conoidea to prevent this dislocation (Fig. 8).

The evolutionary origin of powerful pronation/supination ability in apes highlights the common misconception that there is some fundamental difference between posture and locomotion. The distinction is in reality somewhat artificial; the two grade into one another from the (rare) completely immobile posture, to slow locomotion, to fast locomotion, to extremely fast locomotion with dramatic changes in direction. Some postures require substantial muscle activation, others almost none (Basmajian, 1977).

Related to wrist rotating capacity, apes have a spool-shaped trochlea and a globular capitulum (Fig. 9, Table 5; Tuttle, 1975; Rose, 1983, 1988b, 1993, 1996). The spool shape forms a waisted articulation, the middle portion describing a deep groove bounded medially and laterally by a steep keel. This articulation stabilizes the joint against shear and torsional stresses that tend to dislocate the elbow during vertical climbing, arm-hanging and non-stereotyped locomotion, such as amoebic, quadrumanous movement and scrambling. Such behaviors often involve powerful elbow flexion or rely on elbow stabilization during suspensory locomotion that involves full elbow extension (Sarmiento, 1985, 1987, 1988; Rose, 1988b).

Just lateral to the deeply grooved trochlea is a steeply angled, lateral-facing zona conoidea, which articulates with a corresponding bevel on the articular lateral rim of the radial head; the bevel extends around the entire circumference of the radial head (Rose, 1988b). This angulation (Fig. 8, dotted line D) is part of a pattern of strong relief in the articular surface of the elbow that 'stabilizes the radial head as it rotates *during* pronation and supination' (*ibid*). Because apes can rotate their wrists through 150°, the articular surface on the radial head wraps around the entire head; monkeys, with less rotatory capacity, have an articular surface only part of the way around (Rose, 1988b). The steeply angled zona/radial head bevel would be effective in preventing medial dislocation of the radial head when contractions of the pronators exert forces that squeeze the ulna

and radius towards one another during the sort of dynamic arm-hanging Stern & Larson (2001) described (Fig. 8). In essence, a steeply-angled zona conoidea serves the same function for the radial head that a deeply grooved trochlea plays for the ulna (Sarmiento, 1985, 1987; Rose, 1988b). In sum, a spool-shaped trochlea, a strongly angled zona conoidea and a beveled radial head are adaptations that prevent dislocation of the ulna and radius when powerful moments are generated around the elbow during suspensory behaviors and vertical climbing.

The globular, symmetrical shape of the capitulum allows for rotation of the radial head on the humerus, permitting extensive pronation and supination. The more cylindrical capitular surface and the more trough-like complementary articulation on the radial head of many monkeys limit supination (Rose, 1988b), effectively turning the elbow into a hinge. The limited flexibility allows the radiohumeral joint to bear substantial forces through all angles of flexion and extension of the elbow even as it limits pronation/supination.

As discussed above, the proximal ulna of apes and other suspensory primates has a reduced olecranon process (Fig. 9; Tuttle, 1975; Rose, 1983, 1988b, 1993, 1996). Viewed laterally, the articular surface of the trochlea wraps around posteriorly to end deep in the olecranon fossa. This articular pattern allows for complete elbow extension. If the articular surface extends far enough the olecranon fossa penetrates the humerus creating a stirrup. The perforated olecranon fossa allows the olecranon process of the ulna to further circumduct the trochlea and bear weight during arm-hanging with less support from ligaments; australopithecines frequently evince a perforated olecranon fossa (Stern & Susman, 1983).

The coronoid process of the ulna, just distal to the sigmoid notch, is prominent in apes, projecting ventrally farther than the olecranon process; there is a complementary coronoid fossa on the humerus. The coronoid process increases the moment arm of brachialis when the elbow is fully extended to allow initiation of elbow flexion even when the elbow is completely extended.

A long acromion that extends farther laterally over the humeral head than in monkeys (Tuttle, 1975; Harrison, 1987) increases the lever arm for deltoid. A distally placed deltoid crest, the area of insertion for the deltoid, increases the in-lever for the forelimb during arm-raising. Both are adaptations to reaching out during feeding and to a lesser extent arm-raising during vertical climbing. An elongated coracoid process (Schultz, 1930; Tuttle, 1975; Harrison, 1987) increases the moment arm for biceps, affording more powerful elbow flexion.

Chimpanzees and other hominoids have a large, globular humeral head (Schultz, 1930; Tuttle, 1975; Harrison, 1987) with distally displaced greater and lesser tubercles compared with monkeys (Fig. 10). All three features allow greater shoulder mobility by increasing the angle through

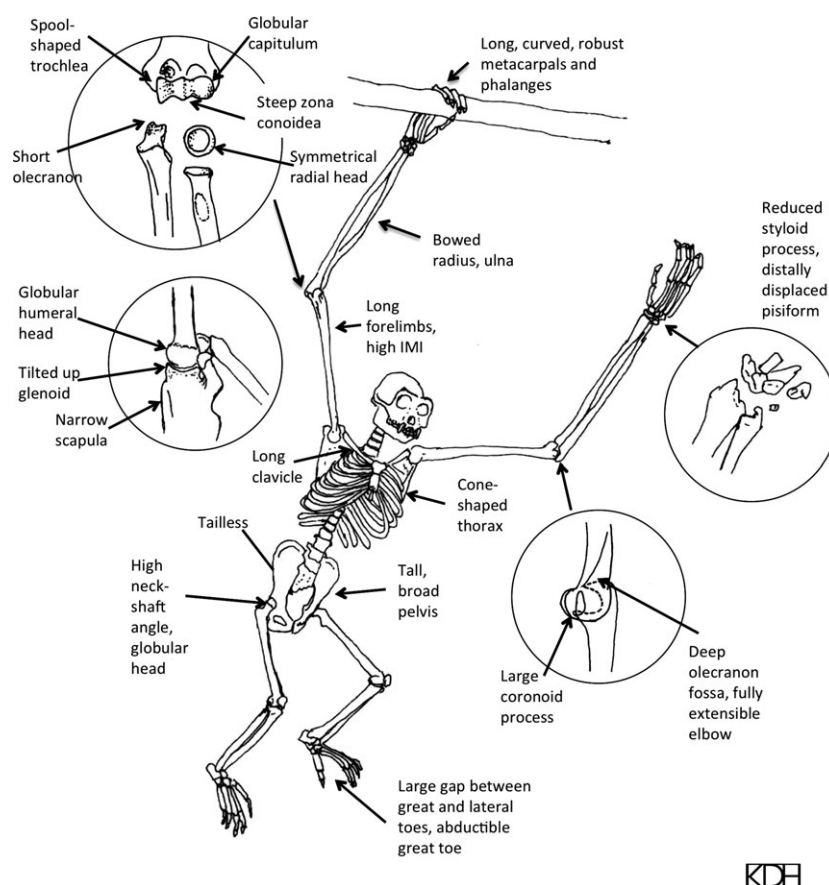


Fig. 9 Ape specializations. A globular capitulum, round symmetrical radial head, reduced ulnar styloid process, and distally displaced pisiform allow free pronation and supination. A bowed radius and ulna increase the moment arms of pronators and supinators. A cranially oriented glenoid fossa reduces strain on the glenohumeral joint capsule during arm-hanging. A globular humeral head allows wide shoulder joint excursion through all three planes. A narrow scapula allows the shoulder joint and the vertebral border to approach the midline during full abduction, reducing strain on the thorax during arm-hanging. A short olecranon process allows complete elbow extension during arm-hanging, and a humeral articular surface for the ulna that wraps completely around the trochlea (dotted line in lateral view of humerus and ulna) allows the body weight to be borne by bone during suspension, rather than muscle, tendon or ligament. A large coronoid process increases the moment arm for brachialis to initiate elbow flexion when the elbow is completely extended. Robust, curved manual rays reduce muscle action during suspensory gripping and reduce stress on the manus. Long forelimbs increase the gathering sphere and aid in vertical climbing. A gripping great toe allows the hindlimb to exert powerful vertical force propelling the body weight upward during climbing. A high neck-shaft angle displaces the femoral head cranially, away from the greater trochanter, to increase hip flexibility. After Fleagle (2013), Rose (1993) and specimens in the Human Origins and Primate Evolution Laboratory, Indiana University.

which the joint can move in all planes. A narrow bicipital groove is hypothesized to enhance mobility as well, presumably by allowing a more globular head and moving the tubercles away from contact with the rim of the glenoid fossa (Corruccini et al. 1976). A large humeral head also distributes stress over a larger area, reducing maximum stress on each square unit. Large, powerful thoracic and forelimb musculature, a large gut and robust skeletal elements generate more stresses in the glenohumeral joint than are generated in hindlimb-powered primates (Kimura et al. 1979).

In lateral view, the glenoid fossa of apes is ovate and uniformly convex and thus more bowl-like (Fig. 11; Schultz, 1930, 1936; Rose, 1993) compared with glenoid of monkeys, which is pear-shaped in lateral view and can be trough-shaped in dorsal view. A bowl-like glenoid fossa and com-

plementary globular humeral head allow the humerus free movement in any direction. Further, an ovate glenoid is more cup-shaped allowing it to resist dislocation on the dorsal and ventral rims, which are in essence absent from the monkey glenoid. Thus, the ovate glenoid resists stress (i.e. bears weight) over a wide range of humeral positions, as is required for a versatile positional repertoire that includes quadrupedalism and suspensory behavior (Roberts, 1974; Rose, 1993). Mobile shoulders (Keith, 1891, 1923; Washburn, 1950) allow the complete abduction required for arm-hanging, and allow large excursions of humerus against the shoulder during suspensory food gathering and suspensory locomotion such as brachiation, clambering, bridging or transferring, or arm-foot-hanging. In a further reinforcement of the shoulder, hominoids have a coraco-

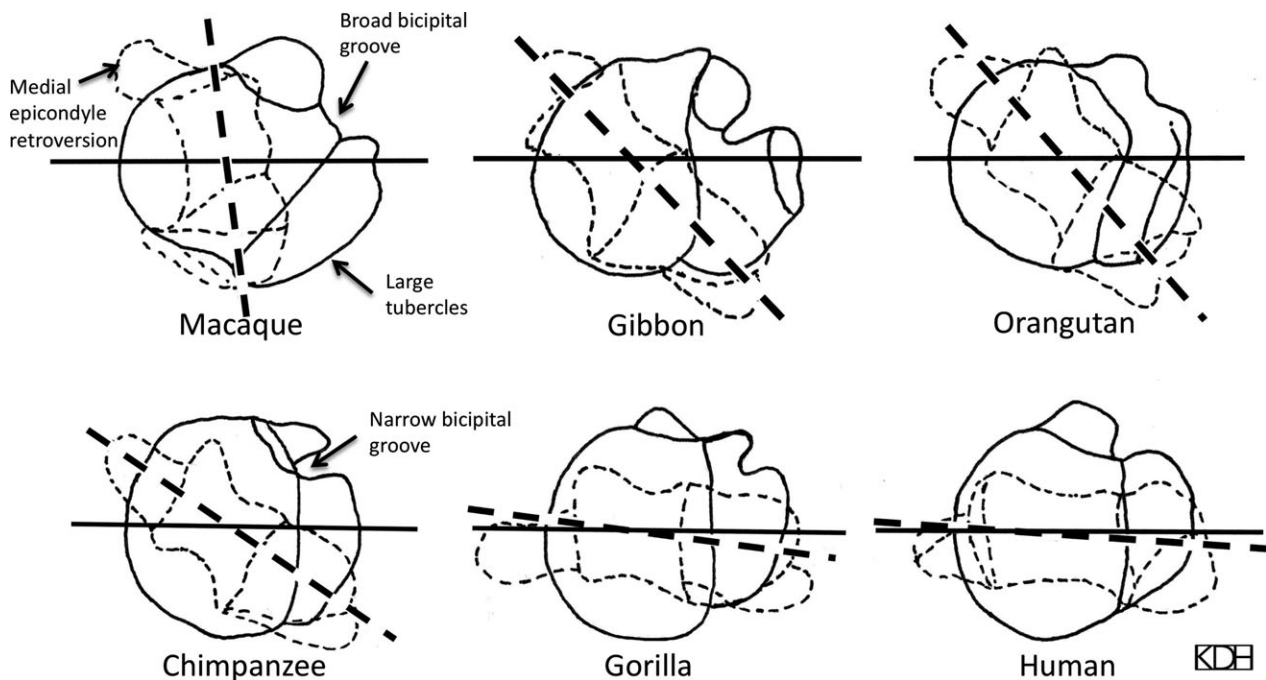


Fig. 10 Cranial view of humerus. Humeral torsion among macaques orients the long axis of the distal humeral articular surface (dotted outline) nearly at a right angle to the direction of the humeral head (solid line). Hominoids have humeral heads oriented medially (solid line) and more nearly parallel to the long axis of the distal humerus (dotted line). Hominoids have large, globular humeral heads that more completely describe a complete sphere. Note the narrow bicipital groove in hominoids and the large tubercles of the macaque. The medial epicondyle of cercopithecoids is retroflexed so that it is caudally directed. After Evans & Krahle (1945).

acromial ligament, hypothesized to prevent vertical dislocation of the humerus, perhaps during suspensory modes (Corruccini & Ciochon, 1976).

The chimpanzee glenoid fossa is tilted cranialward giving the joint a cranial set and raising the caudal rim of the glenoid cranially during complete abduction, such that the glenoid approaches a fully cranial orientation (Hunt, 1991, 1992a). If the fossa were oriented still more cranially the entire circumference of the glenohumeral joint capsule would be under similar tension and would bear weight evenly. The more caudally oriented the fossa is the greater the caudal portion of the capsule must stretch when the humerus is completely abducted, and the less the loose cranial portion of the glenohumeral joint capsule can bear weight (Hunt, 1991; Fig. 4). Chimpanzees appear to be more comfortable with their forelimb above their head than adducted. When sitting, chimpanzees often partly abduct their arm, reaching up to grasp a nearby sapling or overhead branch.

Great apes have both a cone-shaped thorax (Fig. 13) and a mediolaterally broad, dorsoventrally compressed (shallow) ribcage (Fig. 7; Schultz, 1961; Erikson, 1963). Broad thoraxes relocate the scapula to the dorsum (Fig. 7; Schultz, 1950), separate the shoulder joints and orient the glenoid fossae laterally, increasing the excursion of the humerus by removing the chest wall as a barrier (Miller, 1932; Avis, 1962) and allowing shoulder joint excursion across nearly the entire

transverse plane (Schultz, 1960), a kinematic useful during suspensory feeding and locomotion among irregularly placed supports (Schultz, 1936; Ashton & Oxnard, 1964b). Although the chimpanzee thorax is constricted dorsoventrally throughout its length, it is more constricted superiorly both in coronal and sagittal section (Schultz, 1961; Erikson, 1963), yielding a rather cone-shaped thorax compared with the more barrel-shaped ribcage in monkeys (Fig. 13).

The shallow and cone-shaped thorax of chimpanzees and many other suspensory species are hypothesized to be adaptations to reducing compressive forces on the ribcage during arm-hanging (Hunt, 1991). During unimanual arm-hanging, the weight of the body is suspended from a single forelimb, fixed to the thorax via the glenohumeral joint capsule and the scapula. This means the body weight is suspended from a manus and countered by tensile forces in, sequentially, the carpus, ulna and radius, humerus and then finally in part glenohumeral joint capsule. Stress is then most directly distributed to ventral and dorsal anchor points on the thorax; the only lateral connection is serratus anterior. The forelimb is anchored ventrally via the cranial portion of the scapula, the acromion, the clavicle and then anchored to the thorax via the manubrium, and finally indirectly fixed to the sternum ligamentously and finally to the ribs via intercostal connective tissue. Dorsally the forelimb is anchored by passive muscle tension from trapezius, which inserts on the the clavicle, the scapular spine, the cranial

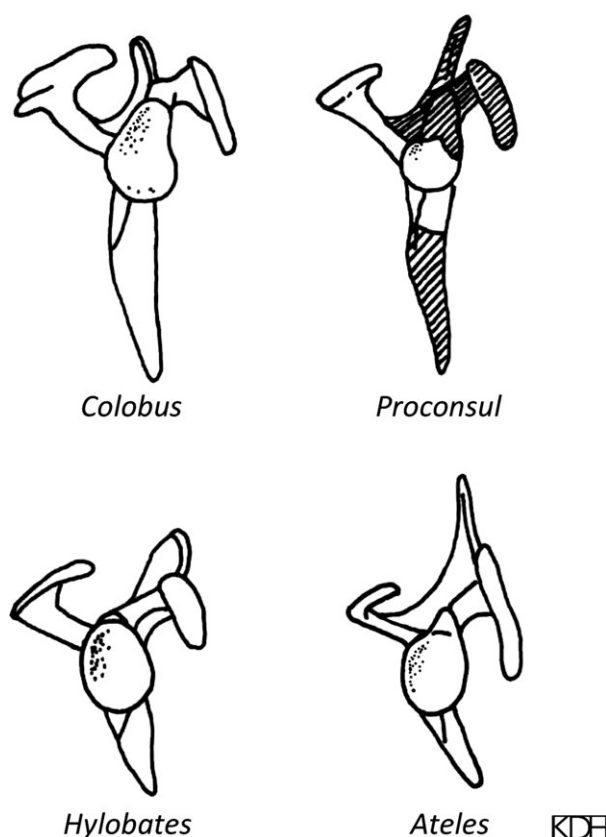


Fig. 11 Lateral view of the scapula. Colobines have a pear-shaped glenoid that can be rather trough shaped. Apes have an evenly concave, bowl-like glenoid that is oval or nearly circular in lateral view. The semi-symmetrical glenoid allows the shoulder joint to resist stress effectively in all three planes, preventing dislocation. The Miocene ape *Proconsul* has a rather monkey-shaped glenoid, whereas the New World suspensory primate *Ateles* is convergent on apes. After Rose (1993).

margin of acromion and the vertebral border of the scapula; other scapula anchors such as teres major and teres minor presumably support body weight by passive elastic tension. A final dorsal anchor, latissimus dorsi, bypasses the scapula and generates tensile force on the humerus through its insertion in the bicipital groove on the proximal humerus; its origin is the spinous processes of the lower vertebrae, the sacrum and the iliac crest. Thus, force generated by the body mass is countered by tensile forces proceeding along the exterior of the thorax.

Together, tensile forces acting on the exterior of the thorax at anterior and posterior anchor points produce dorsoventral compressive forces. The greater the distance between the dorsal and ventral attachment points anchoring the humerus (i.e. strains pressing the sternum and spinal column closer together), the more dorsoventral the compressive forces pressing together the spine and the sternum, resisted by the stiffness of the ribs (Hunt, 1991). The greater the force, the greater the bending stresses on

the ribs. Possibly much lesser compressive forces are exerted mediolaterally by intercostal muscles and ligaments. This compressive force must vary as the body weight is shifted, handholds are changed and adjustments to posture are made; suspensory locomotion acts similarly. Reducing the dorsoventral dimension of the thorax reduces compressive and bending stresses on the ribs and connective tissues, stresses that fatigue muscles and ligaments and have the potential to produce stress fractures. Thus, a cone-shaped thorax is theoretically under less compressive strain during orthograde arm-hanging and has fewer hot spots of high stress than develop in a barrel-shaped thorax. A simple example of these principles can be seen in the observation that a flexible sphere suspended from a single point takes on a teardrop shape.

Jellema et al. (1993) speculated that the cone shape of the ribcage has no adaptive function in and of itself, but is merely an artifact of the broad pelvis of apes. The lower ribcage, in this view, is determined by the breadth of the ilia. If the volume of the thoracic cavity is determined by body mass, the thoracic volume can remain unchanged if a broad lower thorax is matched by a compensating restriction in the upper thorax, resulting in a cone-shaped ribcage. This reasoning is disproven by the anatomy of *Hylobates* and the New World atelines (Fig. 13). Spider monkeys and gibbons have much narrower bi-iliac breadths than lower thoracic breadths, but despite this disparity *Ateles* has a distinctly cone-shaped thorax (Fig. 13).

A shallow thorax is effected by strongly curved ribs (Fig. 3; Schultz, 1960), particularly curved near the costal-vertebral articulation. This shape means the ribs curve in a smaller and smaller radius moving from the sternum to the vertebra. The effect is to leave the vertebral column deeply set in the thoracic cavity. A long clavicle is a consequence of both a broad thorax and the migration of the scapulae to the dorsum (Schultz, 1960). Were the vertebrae not set into the thoracic cavity, dorsoventral depth would be greater, stressing the ribcage more during arm-hanging.

The scapula is anchored ventrally by the clavicle via the acromio-clavicular ligament; the conoid ligament is robust (Swindler & Wood, 1982) to better resist tensile forces during arm-hanging when much of the body weight is borne by this articulation. In chimpanzees and other arm-hangers the clavicle attaches to a particularly broad manubrium (including *Ateles*; Schultz, 1930, 1936, 1961), which in turn articulates with a broad and fused sternum (Schultz, 1950). There has been little speculation concerning the function of the broad manubrium, but it may function to avoid lengthening of an already unusually long clavicle. A longer clavicle is subject to greater bending stresses and is presumably more susceptible to fractures. The long clavicle is in turn a consequence of the broad ape thorax. The fusion of sternbrae is unexplained, but it is consistent with the observation that fusion of separate elements is a scaling trend in that heavier animals tend to fuse weight-bearing elements that

remain separate and linked ligamentously in smaller, related species. The broad thorax, then, may require special structural augmentation to reduce strain, reinforcement that a broad and fused sternum and manubrium offer.

The scapula of unimanual arm-hangers is expanded cranio-caudally and narrow mediolaterally (Fig. 12). To be more precise, the dimension from the glenoid fossa to the caudal edge is long and the dimension from a rather straight axial border to the long but less straight vertebral border is small. The traditional terminology for length and breadth defines length as the mediolateral dimension and breadth as the craniocaudal dimension, a definition that has led some (Larson, 1998) to describe the chimpanzee scapula as broad and others (Hunt, 1991) as narrow; this is merely a terminological issue and both are describing the same phenomenon. This review continues here to use 'narrow' to mean the axial border-vertebral border dimension, and 'long' to mean the dimension from the glenoid fossa and the cranial edge to the caudal border.

Hunt (1991) argued that a narrow scapula is an adaptation allowing a greater excursion of the scapula as it rotates cranially during arm-raising, thus allowing the glenohumeral joint to approach the midline and reducing compressive stress on the thorax (Hunt, 1991). Such a large excursion obviates the need to orient the spinal column at a different angle than the humerus. By allowing the humerus and spine to line up, bending moments on the vertebra are hypothetically decreased as is tensile stress on the weight-bearing side of the thorax. Broader scapula (*sensu* Hunt) in humans, gorillas and orangutans prevent the shoulder joint from approaching the midline during arm-hanging, and these species engage (Fig. 1; Table 3) in

less unimanual arm-hanging and more hand-foot-hanging than chimpanzees, which creates lateral rather than cranial stresses. Orangutans rarely engage in unimanual arm-hanging; instead they often engage in postural and locomotor suspensory behavior in which the thorax is horizontal and the body is suspended from a manus and pes on the same side of the body (Table 3).

A long scapula has been hypothesized as serving as a scapulohumeral force couple, increasing the mechanical advantage of trapezius and serratus anterior during the scapular rotation necessary for arm-raising (Inman et al. 1944; Ashton & Oxnard, 1963, 1964a,b; Oxnard, 1963, 1967). Hunt (1991) argued against such a force couple, reasoning that during arm-raising trapezius is the principal motor rotating the scapula, while the caudal portion of the scapula is uninvolved. Instead, he argued that the scapula was long to compensate for its narrowness; otherwise, the surface area for the origin of infraspinatus would be reduced (Hunt, 1991).

The speculation that there is no force couple (Hunt, 1991) is wrong. Cranial trapezius is almost completely silent during arm-raising, whereas cranial and middle serratus are quite active (Larson et al. 1991; Larson, 2015). Arm-raising, then, is accomplished by firing serratus to rotate the scapula and firing deltoid to rotate the humeral head against the glenoid (Larson et al. 1991; Larson, 2015). Cranial trapezius is silent. The scapula and clavicle thus act as a lever, with serratus rotating the scapula, and the sterno-clavicular articulation serving as the hinge. Serratus pulls the caudal border of the scapula ventrally and somewhat cranially, rotating the scapula with respect to the manubrium and thus raising the arm. Synthesizing the two perspectives, a

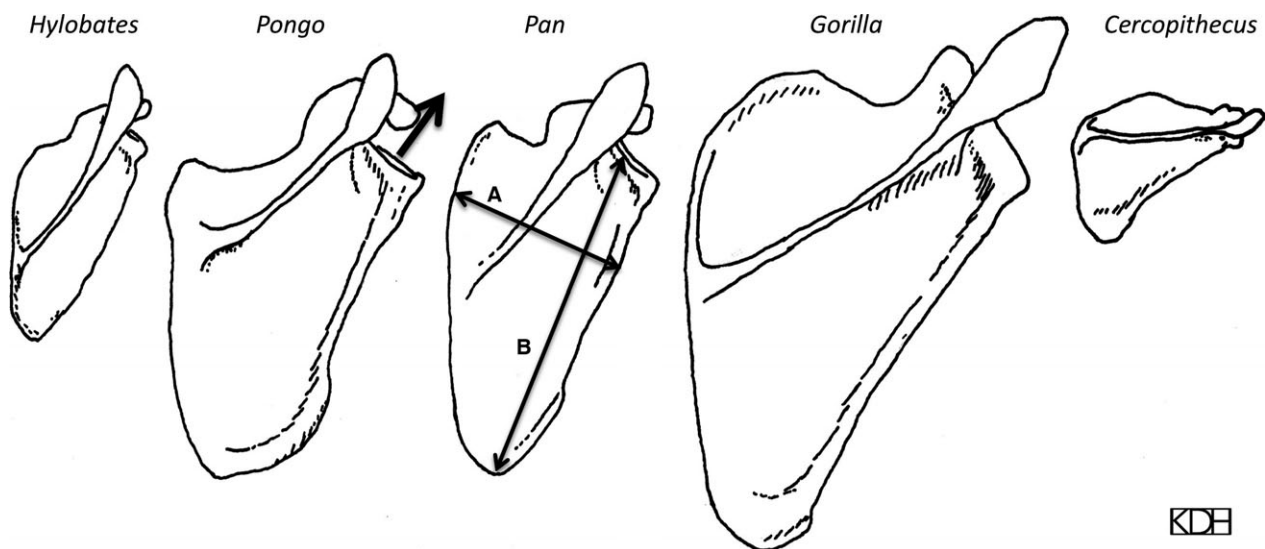


Fig. 12 Dorsal view of scapulae of apes and *Cercopithecus*. Apes have cranially oriented glenoid fossae (arrow on *Pongo*). Chimpanzees and gibbons have 'narrow' (dimension A) and long (B) scapulae. The narrow scapula allows the glenoid to approach the midline, reducing eccentric stress on the thorax; a cranially oriented glenoid reduces strain on caudal fibers of the glenohumeral joint capsule and allows cranial fibers to bear a greater proportion of the body weight than would a laterally oriented fossa. After Larson (1998).

long, narrow scapula serves two functions, it increase the moment arm of serratus during abduction and allows the scapula to rotate through a larger angle, thus allowing the glenohumeral joint capsule to approach the midline.

Among apes the humeral head faces medially and the long axis of the distal humeral articular surface is mediolateral so that the two axes are nearly parallel (Fig. 10). Among Old World monkeys, in contrast, the humeral head faces caudally and the long axis of the distal humeral articular surface is mediolateral, nearly at a 90° angle to the direction of the humeral head (Fig. 10); the complementary glenoid fossa faces cranioventrally (Fig. 12), allowing the elbow to flex so that the forearm moves in the sagittal plane (Rose, 1983). Extant primates with mediolaterally narrow thoraxes have caudal humeral heads and cranially oriented glenoids; those with broad thoraxes have medial heads/cranioventral glenoids (Larson, 1998). The suspensory New World atelines have broad thoraxes and ape-like shoulders (Larson, 1998). Humeral torsion may well be the single most useful measure for interpreting fossil primates as it correlates thorax shape and many other anatomical features, and requires only a reasonably complete humerus for interpretation.

The modal number of chimpanzee lumbar vertebrae is four, compared with five for *Hylobates* and 4.6 for *Symphalangus* (Schultz, 1933). The lumbar vertebral bodies are short and broad compared with monkeys (Fig. 13; Schultz, 1961; Ankel, 1967; Benton, 1967). Furthermore, the vertebrae are invaginated or depressed inferiorly (or caudally) so that one and sometimes two lumbar vertebrae are completely caudal to the iliac crest. The great ape lumbar spine is so short that the last rib nearly touches the iliac crest (Fig. 13), whereas in Old World monkeys the gap is large (Fig. 2). In concert with the reduced lower back, chimpanzees (and other great apes) have an elongated os coxa (Fig. 13; Schultz, 1933). The consequence is that the lower back is constituted by a nearly non-existent lumbar spine and a completely inflexible pelvis. This stiff, largely immobile back is best explained as resisting buckling strain produced during vertical climbing generated by two forces: a propulsive or cranially directed force generated by the hindlimbs (Ward, 1993; Jungers, 1984); and a lateral bending force generated by the action of latissimus dorsi (Sonntag, 1923; Waterman, 1929; Gregory, 1950). When a hindlimb is pushing the body upward at the same time that an ipsilateral forelimb is pulling the body upward, the powerful latissimus dorsi and the propulsive impulse from the hindlimb bends the spine in the same plane, placing tremendous bending moments on the lumbar vertebrae in particular (Ward, 1993). It is not known how much of the gait cycle during vertical climbing consists of ipsilateral forelimb and hindlimb impulses, but it is substantial enough that it is likely that a short lumbar vertebral segment is an evolutionary response to this stress. Tuttle &

Basmajian (1977) hypothesized that a short torso and an iliac origin of latissimus dorsi together serve to form a direct link between the lower body and the humerus during climbing.

Among chimpanzees, vertical climbing is the most distinctive behavior for which a short lumbar region has been hypothesized, but settling into and out of either arm-hanging or non-stereotypical postures (postures with eccentric or extreme joint angles) among unpredictably oriented and erratically sized supports may stress the back as well (Ward, 1993). Chimpanzees do not engage in bridging behaviors in which the hindlimbs hold the lower body rigid as the forelimbs reach out for a handhold in an adjacent tree (Hunt, 1991, 1996; see Fig. 10 for an illustration of this type of bridging); instead their transferring locomotion, while sometimes called bridging, involves unimanual or bimanual suspension.

The ilium of great apes is broad as well as long (Fig. 13; Schultz, 1933), a feature quite noticeable in ventral view and among the greatest differences between monkeys and apes. This feature may result from the same selective pressure that has resulted in a short lumbar spine, but it is conceivable that a primate might have both a tall pelvis and a long lumbar vertebral segment. Stern (1971) speculated that a tall, broad ilium is a result of selection for a large iliac surface area, an allometric compensation to maintain mechanical competence of the gluteals in the face of increasing body weight. A broad ape pelvis is the mechanical equivalent of the narrower monkey pelvis, given larger ape body masses and the constraints of the square-cube law. The gluteals are active in stabilizing the hip during leaping (Stern, 1971), and extending the hip during vertical climbing and running (Fleagle et al. 1981). This allometric explanation (Stern, 1971) accounts for large ape iliac blade surface areas, but cannot explain the extended isthmus in the great ape os coxa, which yields an elongated pelvis, not simply a broad or tall one. It seems more likely that the tall os coxa with an elongated isthmus is completely attributable to selection for reducing buckling forces during vertical climbing; by dedicating more of the length of the back to the inflexible os coxa and less to the flexible vertebrae a long isthmus stiffens the back. To the author's mind, the ape short lumbar segment and tall pelvis is the most important ape specialization yet to be satisfactorily explained.

Stern's (1971) hypothesis that the broad iliac blade is an allometric consequence of larger body size is supported by a comparison between gibbons and siamangs (Fig. 13). The smaller gibbon has a narrow iliac and bi-iliac breadth, whereas the siamang, at twice the body weight of gibbons, approaches the form of the great apes (Fig. 13; Schultz, 1933). Another comparison, between two gibbons, fits this hypothesis, as well; the heavier *H. klossi* has a broader pelvis than *H. lar* (Schultz, 1933).

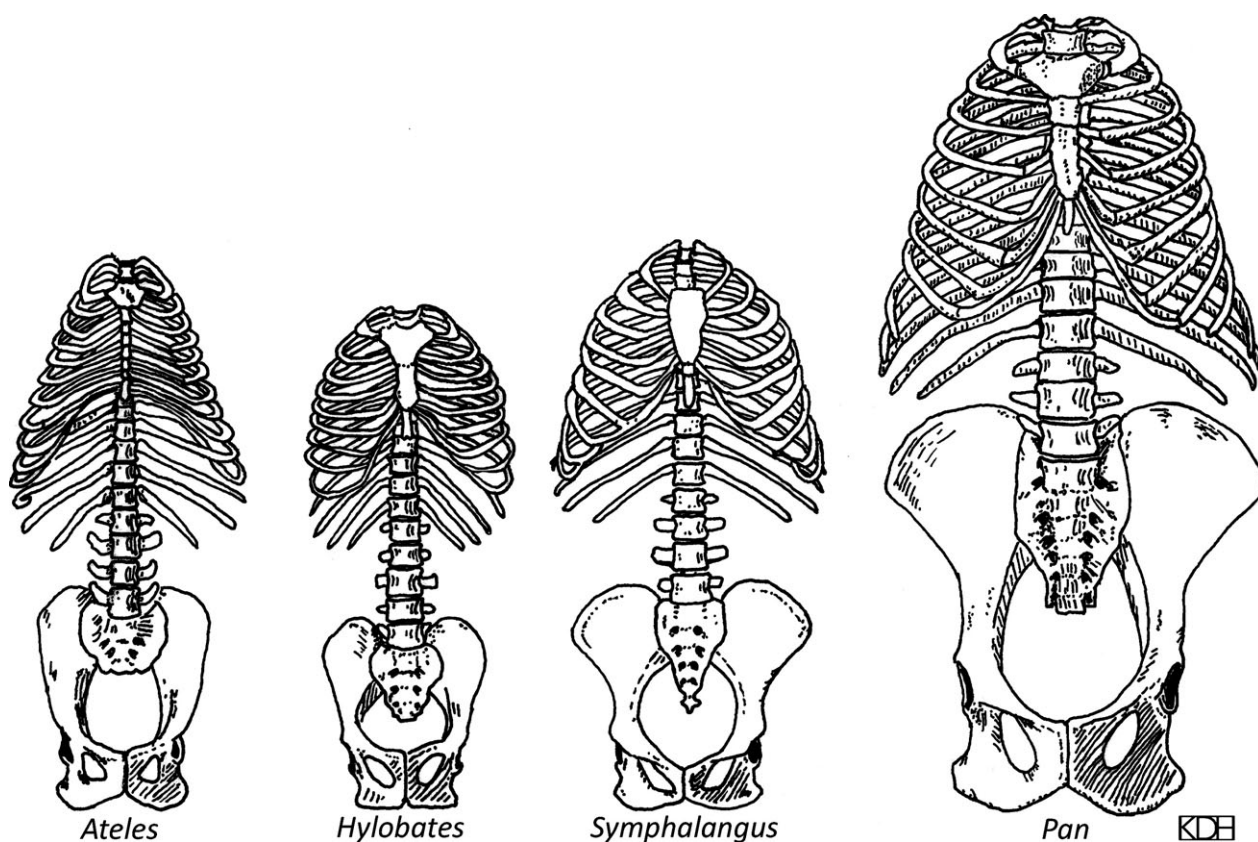


Fig. 13 Ventral view of thoraxes of (L–R) the spider monkey, the gibbon, the siamang and the chimpanzee (to scale). All are arm-hangers (Fig. 1; Table 3) and possess narrow scapulae (Fig. 12). The siamang thorax is more cone shaped than that of gibbons, though both engage in high frequencies of arm-hanging (Fig. 1; Table 1), suggesting that there is an allometric component to the cone-shaped ribcage, with the lighter gibbon requiring less accommodation to forces acting on the thorax. Note also that the thoraxes of spider monkeys and gibbons are broader than the pelvis, demonstrating that the breadth of the caudal border of the ribcage is not determined by pelvic width. The spider monkey thorax shows that the cone-shape is not merely a consequence of pelvic width, but likely has some adaptive value. Stern (1971) suggested that pelvic breadth and thus surface area of the ilium has an allometric component, and that selection to maintain mechanical equivalence requires a disproportionate expansion of the ilium to accommodate allometrically expanded hip extensors. The contrast between the gibbon pelvis and that of the siamang, which resembles the great apes, supports this explanation. Note also that the siamang is convergent on great apes not only in thorax shape and pelvic breadth, but in sacral breadth and lumbar vertebral number as well; gibbons typically have five lumbar, but siamangs have four as often as five (Schultz, 1933). *Ateles*, *Hylobates* and *Pan* after Schultz (1950); siamang after Schultz (1936, 1960), specimen 'Joey' at U of Oklahoma Natural History Museum and specimens in the Human Origins and Primate Evolution laboratory, Indiana University.

In support of the buckling hypothesis, siamangs have shorter, broader lumbar vertebrae than gibbons; whereas gibbons have five lumbar vertebrae, siamangs (*Hylobates syndactylus*) have only 4.6 (Schultz, 1933; Table 9), convergent on great apes.

Great apes also have a narrow sacrum, a feature for which no function has been proposed. The author proposes that the narrow sacrum is a consequence of the same selective forces Stern proposed for the broad ilium. A narrow sacrum leaves greater surface area for the hip extensors without increasing pelvic (bi-iliac) breadth. A comparison of the siamang and gibbon supports this hypothesis: the larger siamang has both a broader pelvis and a narrower sacrum (Fig. 13).

Perhaps the best working hypothesis is that iliac length (i.e. pelvic height) and short lumbar segments function to

resist buckling forces during vertical climbing, and a broad pelvis and narrow sacrum are allometric responses that maintain femoral extension capabilities in species with larger body masses. The heavier siamang has positional behavior and habitat use that converges on that of the orangutan (Fig. 3; Table 1; Collis et al. 1999), further suggesting that body mass and its allometric correlates help to explain great ape pelvic breadth and lumbar morphology.

The femoral head of apes is large and globular; it encompasses three-quarters of a sphere compared with the hemispherical femoral head in monkeys. Ape femoral heads are cranially displaced by a high neck-shaft angle; or alternatively it might be said that the greater trochanter is distally displaced (Fig. 14). A large femoral head, because the joint surface nearly describes a sphere, allows large joint excu-

sions so that the femur can describe a wide range of angles in all three planes (Walker, 1974; Fleagle, 1976b; Harrison, 1982; Dagosto, 1983; Stern & Susman, 1983; Fleagle & Meldrum, 1988; Anemone, 1990; MacLachy & Bossert, 1996). The distal displacement of the greater trochanter removes a barrier to these large excursions, whereas a cranially extended trochanter would encounter the rim of the acetabulum during abduction with smaller angular displacement than a distally displaced trochanter. Orangutans have the greatest hip flexibility of all primates and they often engage in behaviors requiring it, including the lateral hand-foot hang, and a suspensory behavior where all four limbs are fully abducted while the thorax is orthograde so that all grips occur at or above the head (Fig. 1; Table 3).

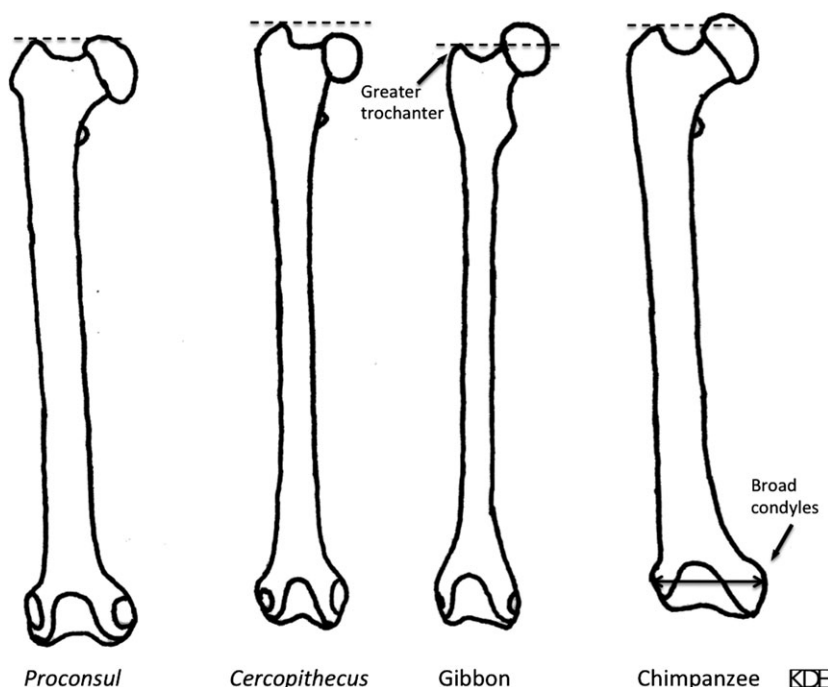
The distal femoral condyles of apes are broad, yielding a mediolaterally expanded knee joint. This may be an adaptation to cope with higher mediolateral bending moments about the knee generated by the broad ape thorax. Alternatively, but perhaps less likely, wide knee joints may be an allometric effect of larger ape body masses. That is, due to the square-cube law a disproportionally broad knee may be necessary among larger primates to counter disproportionally larger forces generated during locomotion. Variation in pelvic breadth, body mass, IMI and other morphological features among the various species in the genus *Hylobates* (Fig. 13) would allow a test of hypotheses related to this and other allometric contrasts in the apes.

All apes have abductible, gripping great toes, and all except the orangutan have long, robust first pedal rays (Fig. 3; Schultz, 1936, 1963; Tuttle, 1970; Rose, 1988a) and all have ventrally curved, phalanges. A gripping pes is

adapted to vertical climbing near-vertical, relatively rigid supports of 3–10 cm in diameter, but the gripping great toe is little-recruited when walking on sub-horizontal arboreal supports. During knuckle-walking on large (10 cm diameter) supports, neither the pes nor the manus grips the substrate; on intermediate sized branches the great toe may grip the substrate, but just as often does not. During pronograde locomotion on smaller supports either the lateral toes alone or the plantar surface contacts supports, but the hallux does not appear to aid in gripping. Small (1–3 cm) supports are compliant and often deform under body weight to near-vertical, whether in posture or locomotion. On such small supports the great toe is of little use in gripping and therefore is rarely recruited; weight is borne by the lateral toes alone; the foot is often dorsiflexed (personal observation). It may be that orangutans grip supports during climbing with the lateral toes but not a power grip using the hallux; or hindlimb propulsion may be insignificant; or support diameters may differ between chimpanzees and orangutans; or the calcaneus may function as a hallux (Sarmiento, 2012); or the long phalanges may substitute for a gripping hallux.

Apes are tailless. That the tail plays a critical role in maintaining balance on narrow or unstable supports is settled science (Buck et al. 1925; Russo & Shapiro, 2011). By whipping the tail back and forth the progressing animal makes minor adjustments to balance to better maintain the center of gravity directly above support. Arboreal animals locomote on supports where a tail would be of use, requiring some explanation for the loss of the tail among apes. The exact timing of the loss is not known (for review, see Russo & Shapiro, 2011) but by ~20 Ma, the basal hominoid *Procon-*

Fig. 14 Ventral view of femora of the Miocene ape *Proconsul*, the African arboreal monkey *Cercopithecus*, the gibbon and the chimpanzee. Chimpanzees and gibbons have a cranially angled femoral neck resulting in a femoral head that rises above the greater trochanter (dotted line). The distal displacement of the greater trochanter allows for greater hip mobility particularly in abduction. A cranially extended greater trochanter increases the length of the moment arm for hip extensors; powerful hip extension increases the velocity and ultimately the distance of a leap. Apes have broad femoral condyles, perhaps to resist bending moments in the transverse plane during the propulsive phase of vertical climbing. After Rose (1993).



sul almost certainly lacked a tail (Ward et al. 1991; see below for further discussion of the phylogenetic status of *Proconsul*).

Tail reduction is at least partly an allometric phenomenon, as the heaviest Old World monkeys have reduced or even absent tails (Fleagle, 2013). Early apes may have lacked tails for two reasons. First, slow, cautious movement with multiple contacts with the substrate would obviate the need for a tail, and early Miocene ape morphology suggests adaptations to slow cautious movement, compared with extant monkeys (Table 2). Second, large body size may select against tails. While tails are not one-dimensional, much of their volume is generated by greater length, which increases the force the tail exerts on the body to maintain balance. Because the force generated to aid balance must scale to body mass, larger animals require a disproportionately longer, heavier tail. There may be a tipping point where the weight and length of a long tail is not worth the predation risk and energetic cost of carrying it. Early Miocene apes are large compared with most monkeys; even the smallest species of *Proconsul* is large in monkey terms; *P. heseloni* females weigh 9.8 kg (Table 2), more than the tailless Celebes macaque (*Macaca nigra*: female body mass 5.5 kg; Fleagle, 2013) and equal in weight to female savanna baboons (*Papio anubis*: 11.2 kg; Table 2), which have quite reduced tails. Female body masses for other species of *Proconsul* are even larger, estimated as ranging from 30.0 to 63.4 kg. If the earliest tailless apes were at the midrange for *Proconsul*, body size alone can explain ape taillessness, and even *P. heseloni* was heavy enough to suggest tail loss is explained by body mass.

Muscular adaptations

A revelation in the study of chimpanzee and ape functional morphology was the discovery that most muscles that cross the shoulder joint or fix the scapula to the thoracic wall are silent during arm-hanging (Tuttle & Basmajian, 1974, 1977, 1978a,b). The well-established brachiating hypotheses held that these 'brachiating muscles' were adapted to suspensory locomotion and/or suspensory posture and therefore were quite active during suspensory behavior (Keith, 1891, 1923; Schultz, 1930, 1936, 1953, 1963; Washburn, 1950; Ashton & Oxnard, 1963, 1964a,b; Erikson, 1963; Napier, 1963; Oxnard, 1963, 1967; Ashton et al. 1965). As Tuttle and Basmajian were publishing their surprising reports, the strength of the brachiation paradigm was already being eroded by reports that brachiation was rare in wild chimpanzees (Goodall, 1963; Reynolds & Reynolds, 1965). In light of Basmajian's (1977) muscle-sparing hypothesis, the quiescence of 'brachiating' muscles during arm-hanging is powerful support for the contention that chimpanzees have a highly evolved adaptation to suspensory behavior.

Chimpanzees and other apes are distinguished by large PCSAs and thus powerful muscles that flex the elbow, retract the humerus and raise the arm (Table 6; Ashton & Oxnard, 1963, 1964a,b; Napier, 1963; Oxnard, 1963, 1967; Ashton et al. 1965; Tuttle, 1969). Latissimus dorsi, caudal and sternocostal pectoralis major, posterior deltoid, caudal pectoralis major, lowest caudal serratus anterior and teres minor are larger in chimpanzees than monkeys (Table 6); these muscles are very active during humeral retraction (= extension), a hoisting or pull-up action engaged in during vertical climbing and during suspensory locomotion and when moving in or out of arm-hanging postures (Tuttle, 1969); these actions are less common and presumably require less power than is required in vertical climbing. Biceps brachii, brachioradialis and brachialis are large in chimpanzees and very active in elbow flexion (Table 6). Retracting the humerus and flexing the elbows are the two important actions of the upper body during vertical climbing and are likely well-developed in apes as an adaptation to this mode.

Cranial pectoralis is active in rapid non-weight-bearing protraction of the arm during climbing, and anterior and middle deltoid and middle caudal serratus anterior are active during both abduction and protraction, suggesting that large PCSAs in these muscles are adaptations to behaviors peculiar to apes. Clavicular pectoralis major and caudal trapezius are likewise active during the same motions. Chimpanzees recruit these muscles when reaching out during feeding or when lifting the arm during vertical climbing. While feeding typically makes up half of the primate active period, vertical climbing constitutes less than 1% of the daily active period (Hunt, 1992a), which might be seen as supporting the hypothesis that these muscles evolved large PCSAs as an adaptation to terminal branch feeding. Despite the low frequency of climbing locomotion, however, vertical climbing requires greater muscle recruitment than arm-hanging, requiring not only muscular activity to maintain shoulder flexion, but also decelerating the trailing limb and accelerating it cranialward to reach the next support. These muscles are most likely adapted for both activities.

Lower caudal serratus anterior, supraspinatus and infraspinatus are active during both humeral retraction and during arm-hanging, and likely are particularly powerful among apes as an adaptation to both behaviors (Table 6), though the precise role these muscles play during these actions deserves further study.

While comparisons with monkeys are not yet available, chimpanzee and bonobo muscle architecture is characterized by large PCSAs in muscles of hindlimb extension (Payne et al. 2006), also likely an adaptation to vertical climbing.

Low cusps, thin enamel and long shearing crests of chimpanzees (Kay, 1977; Martin, 1985) are adaptations to a diet of ripe fruit with foliage as fallback foods.

Table 6 Muscle size and function in great apes.

Muscle	Comparative size	Active during humeral retraction	Active during walking	Active during arm-hanging	Active in protraction or abduction	Active in elbow flexion	Likely adaptation
Biceps brachii	Ape >>> monkey ¹	— ²	— ²	— ²	— ²	+++ ²	VC
Brachialis	Ape >> monkey ¹	— ²	— ²	— ²	— ²	+++ ²	VC
Brachioradialis	Ape > monkey ¹	— ²	— ²	— ²	— ²	+++ ²	VC
Deltoid	Ape >>> monkey ^{1,3}						
Anterior		+ ⁴	+ ^{5,6,7}	++ ⁴ , — ⁸	++ ^{3,4,5,6,9}	— ¹⁰	VC, AH
Middle	Ape >>> monkey ¹¹	— ⁴	+ ^{5,6,7}	++ ⁴ , — ⁹	+++ ^{4,9}	— ¹⁰	VC, AH
Posterior		+++ ⁴	++ ^{9,7}	+ ⁴ , — ⁹	— ^{4,5}	— ¹⁰	VC
Digital flexors	Ape >>> monkey ²	— ²	+ ²	+++ ²	— ²	— ²	AH
Infraspinatus	Ape > monkey ^{3,4}	— ^{3,4,9}	+ ^{5,6,7}	+++ ⁴ , — ^{8,12}	++ ^{3,4,5,9}	— ¹⁰	VC, AH
Latissimus dorsi	Ape >>> monkey ^{7,15}	+++ ^{4,3}	— ^{7,12}	— ^{9,13}	— ^{9,13}	— ¹⁰	VC
Pectoralis major	Ape >>> Monkey ¹⁶						
Clavicular		— ⁵	— ^{5,6}	— ¹³	+++ ^{3,13}	— ¹⁰	VC, AH
Sternocostal		++ ¹³	++ ^{6,7}	— ¹³	— ¹³	— ¹⁰	VC
Caudal		++ ¹³	++ ^{6,7}	— ¹³	— ¹³	— ¹⁰	VC
Pectoralis minor	Ape = monkey ¹⁵		++ ^{5,6}			— ¹⁰	0
Pronator teres	Ape >> monkey ¹⁹	— ¹⁷	— ¹⁷	+++ ¹⁷	— ¹⁷	— ¹⁷	AH
Pronator quadratus	Ape >> monkey ¹⁹	— ¹⁷	— ¹⁷	+++ ¹⁷	— ¹⁷	— ¹⁷	AH
Rhomboids	Ape > monkey ¹¹	— ⁹	+ ⁷	— ⁷	— ^{3,9}	— ¹⁰	X
Serratus anterior							
Middle caudal	Ape >> monkey ^{15,16}	— ¹⁴	— ⁷	++ ¹⁴ , — ¹³	++ ^{5,13,14}	— ¹⁰	VC, AH
Lowest caudal	Ape >> Monkey ^{15,16}	+++ ¹⁴		++ ⁶	— ¹⁴	— ¹⁰	VC, AH
Subscapularis	Ape < monkey ^{3,4}	+++ ⁵	+ ^{5,6,7}	— ⁹	+ ^{18,7}	— ¹⁰	0
Supinator	Ape >> monkey ¹⁹	— ¹⁷	— ¹⁷	+++ ¹⁷	— ¹⁷	— ¹⁷	AH
Supraspinatus	Ape > monkey ⁴	++ ⁹	++ ^{6,7}	— ⁹	+++ ^{5,6,9}	— ¹⁰	VC, AH

Evidence for competition and co-evolution between apes and monkeys

Extant ape and monkey ecomorphology

Andrews (1981) was the first to speculate on the deep-time evolutionary implications of the ape/monkey dietary dichotomy. He noted that greater species numbers among extant monkeys is a relatively recent phenomenon, and found a striking negative correlation between ape and monkey species numbers over time (Fig. 15). Temerin & Cant (1983) proposed that the apes evolved adaptations for harvesting relatively dispersed, patchier but higher quality food patches by traveling more efficiently or faster and by relying on suspensory behavior, whereas monkeys evolved bilophodont teeth to allow them to exploit lower-quality food items.

Extant monkeys far outnumber extant apes. In Asia and Africa there are 136 species of monkeys (Tables 1 and 2) yet only 20 species of apes, and 14 of these species are hylobatids. In Africa there are four species of great ape and 71 species of monkey. Multiple species of monkeys are found in all ape habitats. In Campo-Ma'an, Cameroon, 11 species of monkeys are sympatric with two apes, gorillas and chimpanzees (Matthews & Matthews, 2002). The bias is similarly pronounced for population density. Chimpanzees are found

at densities of approximately one individual per km² (Smuts et al. 1986), whereas monkey densities are an order of magnitude higher. In Uganda, a survey of eight conservation areas with endemic primates reported monkey species numbers averaging 12 vs. 1.4/km² for chimpanzees. The total number of monkeys was 86 vs. 1.4/km² for chimpanzees (Plumptre & Cox, 2006). Numbers are similar at other sites (Smuts et al. 1986).

Competition for food may be direct, but even when monkey species are not seen at the same feeding sites as chimpanzees at the same time, competition can be intense. Diets overlap extensively (Table 7). MacKinnon & MacKinnon (1978) found that there was up to a 35% overlap of food items between hylobatids and *Macaca fascicularis*. Siamang (body weight 10 kg) diets are 44% fruit; gibbons (5 kg) diets are 59.6% fruit and fruit makes up 64.9% of macaque (3 kg) diets. At the Kibale Forest, four monkey species overlapped in feeding time on ripe fruits – the most highly selected and most common chimpanzee food – 71.8% of the time (Wrangham et al. 1998). Of 34 species of fruits commonly surveyed at Kibale, only two were eaten by chimpanzees alone, while 32 were eaten by both chimpanzees and monkeys (Wrangham et al. 1998). The chimpanzee diet is to a great extent a subset of the monkey diet, with monkeys at Kibale eating a further 21 species of fruit that chimpanzees did not (Wrangham et al. 1998).

Table 6 (continued)

Muscle	Comparative size	Active during humeral retraction	Active during walking	Active during arm-hanging	Active in protraction or abduction	Active in elbow flexion	Likely adaptation
Teres							
Major	Ape = monkey ^{3,15}	+++ ^{4,13}	— ⁷	— ^{5,9}	— ¹³ , + ¹⁸	— ¹⁰	0
Minor	Ape > monkey ⁴	— ⁵	— ^{6,7}	++ ⁵ , — ⁷	— ⁵	— ¹⁰	VC
Trapezius							
Cranial	Ape >> monkey ^{1,3,15}	— ¹³	— ⁷	— ¹³	— ¹⁴	— ¹⁰	X
Caudal	Ape >> monkey ¹	+ ²⁰	— ⁷	+ ¹⁴	+++ ¹⁴	— ¹⁰	VC, AH
Triceps	Ape << monkey ¹⁶	— ¹³	+ ²	— ²	+ ²	— ²	0

Relative muscle size: while relative PCSA would be the most accurate means of comparison (Thorpe et al. 1999), comparative PCSAs between monkeys are not often available. Following Larson (2015), proportional comparisons of muscle size were assumed to be valid despite variation in methodology and approach. Comparative size is estimated from size of individual muscles in relation to a larger muscle group, typically forelimb and thoracic muscles. Where not indicated otherwise, comparisons are between all apes and a variety of monkeys (see individual works for monkey species).

Likely adaptation: **Bold face:** an adaptation to a single positional behavior is suggested. Underline: adaptation to two behaviors suggested. Positional mode followed by a query: some data missing, but adaptation likely. Where results are diametrically opposed, two values are given; an attempt was made to give a single value if possible. 0, muscle size smaller in apes, so no behavioral specialization identifiable; X, too little data, or not distinctive; VC, vertical climbing; AH, arm-hanging or reaching during arm-hanging. EMG activity: +++ marked in most or all studies; ++ variably high (by study or experiment) or consistently moderate; + low or variably moderate; — inactive in most studies or very low activity; — — inactive in all studies. Muscle size: >>> much larger in apes by most measures; >> larger in apes by most measures; > somewhat larger in apes by most measures; 0 no larger in apes or activity inconsistent; = no significant difference between apes and monkeys; < smaller in apes or variably smaller according to measure; << much smaller in apes in most studies.

¹Relative muscle mass; comparative species are all five ape taxa, hylobatids, *Pongo*, *Gorilla* and *Pan* compared with *Macaca*, *Cercopithecus mona*, *Papio* and *Cebus* (Miller, 1932).

²Tuttle et al. (1983).

³Relative muscle mass; *Hylobates* and *Pan* compared with *Macaca* (Inman et al. 1944).

⁴PCSA comparison of *Pongo*, *Gorilla*, *Pan*, *Symphalangus* and *Hylobates* compared with *Chlorocebus*, *Cercopithecus* and *Macaca* (Larson, 2015).

⁵Larson & Stern (1986).

⁶Larson & Stern (1987).

⁷Tuttle & Basmajian (1978b).

⁸Larson & Stern (2013).

⁹Tuttle & Basmajian (1978a).

¹⁰Few tests have been conducted isolating elbow flexion from 'pull-up' and climbing behaviors that include humeral protraction, but EMG on humans where flexion is isolated suggests low activity for these muscle groups (Basmajian, 1977; Aiello & Dean, 1990).

¹¹Corruccini & Ciochon (1976).

¹²Larson & Stern (2013).

¹³Tuttle & Basmajian (1977).

¹⁴Larson et al. (1991).

¹⁵Relative muscle mass; *Pongo*, *Gorilla*, *Pan*, *Symphalangus* and *Hylobates* compared with 13 cercopithecines (Ashton & Oxnard, 1963).

¹⁶Relative muscle mass; *Pongo*, *Gorilla*, *Pan* and *Hylobates* compared with *Cebus*, *Callithrix*, *Papio*, *Cercopithecus* and *Macaca* (Oxnard, 1963).

¹⁷Stern & Larson (2001).

¹⁸Jungers & Stern (1980, 1984).

¹⁹Relative muscle mass; species as in (p) (Oxnard, 1963; Lewis, 1969).

²⁰Larson & Stern (2007).

Wrangham and colleagues (Wrangham, 1977, 1979, 1980; Wrangham et al. 1998; Conklin-Brittain et al. 1999) have hypothesized that monkeys are able to sustain a more diverse diet because they tolerate high levels of antifeedants such as tannins, alkaloids and terpenes. Particularly important for ape/monkey competition, the ability of monkeys to tolerate chemical antifeedants allows them to eat unripe fruits (Wrangham, 1980; Wrangham et al. 1998).

Consuming fruits earlier in the fruiting cycle allows monkeys to avoid direct or contest competition with apes where their diets overlap. Adaptations that allow the consumption of unripe fruit with its attendant antifeedants preadapted the precursors of the colobines to specialize on high-cellulose, high-secondary compound mature leaves, as leaves contain high concentrations of tannins and cellulose (Conklin-Brittain et al. 1999). The first fossil monkeys appear at

19 Ma (Benefit, 1999) and, presuming that a suite of anti-feedant adaptations that allow consumption of unripe fruits was a preadaptation to folivory, antifeedant tolerance must have evolved substantially by the appearance of the colobines at 16.2 Ma (Table 8).

The respective foraging strategies and therefore positional behavior of monkeys and apes are dictated by their differing abilities to cope with antifeedants (Wrangham, 1979, 1980). Tolerance of high levels of secondary compounds and high cellulose contents means blossoms, new leaves, mature leaves, petioles, chemically protected insects and unripe fruit make up a diverse monkey diet

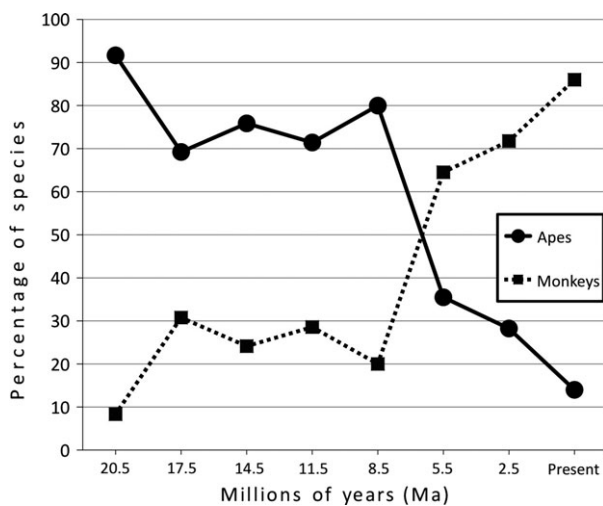


Fig. 15 With a brief hiatus from 8–10 Ma, monkey species numbers steadily increased at the expense of apes. Increasing species numbers, population numbers and niche pressure hypothetically drove a shift in apes from a sit-to-feed, feed-as-you-go adaptation in the early Miocene to their current walk-climb-arm-hang adaptation. After Harrison (2010b).

that also includes ripe fruit. This broad and eclectic diet means monkeys can find edible foods in a higher proportion of trees and allows them to harvest foods in a feed-as-you-go manner, sitting to feed in the core of the tree canopy, then leaping to the next tree (Ripley, 1967, 1979) where they are much more likely than chimpanzees to find edible items. Even though walking on the ground might be more efficient than walking and leaping in trees, when an adjacent tree is likely to contain edible items it is more energetically efficient to travel arboreally than to expend the calories necessary to descend, walk and reascend.

Because ripe fruit is dispersed, chimpanzees face a challenge quite different than that confronting monkeys. Adjacent trees are much less likely to contain edible food resources, thus requiring longer locomotor bouts between feeding sites. Because arboreal locomotion is more expensive than terrestrial locomotion, longer locomotor bouts required to reach dispersed resources are more energetically expensive than descension, travel and reascension (Pontzer & Wrangham, 2004). Whereas monkeys fall back on unripe fruits, leaves and tannin-rich seeds when ripe fruit is scarce (Lambert et al. 2004; Marshall & Wrangham, 2007), chimpanzees fall back on low tannin, low toxin piths, immature leaves and mechanically defended food items, a substantial portion of which can be harvested terrestrially. Thus, chimpanzees have evolved a terrestrial travel adaptation (knuckle-walking) and an arboreal feeding regime that involves vertical climbing and arm-hanging. Rather than feed-as-you-go, chimpanzees have evolved a walk, climb, sit-when-you-can, arm-hang-when-you-must adaptation that also augments arboreal food items with terrestrial resources encountered incidentally during travel.

The early evolution of larger ape body sizes (Tables 1, 2, 5 and 8) suggests that larger body mass may have been the

Table 7 Ape vs. monkey diets (% time feeding).

Site	Insects	Leaf	Meat	Fruit	<i>Pennisetum</i>	Other ¹
Gombe chimpanzee ²	4.0	24.0	< 1.0	60.0	0.0	15.0
Gombe chimpanzee ³	3.4	16.6	0.3	63.3	0.0	16.5
Mahale chimpanzee ⁴	5.9	10.6	0.9	56.7	19.1	6.0
Redtail ⁵	21.8	15.5	0.0	43.6	0.0	19.4 ⁶
Blue Monkey ⁷	19.8	18.7	0.0	42.7	0.0	18.4 ⁸
Mangabey ⁹	10.9	5.3	0.0	58.8	0.0	9.9 ¹⁰

¹Including blossoms, bark, soil, seeds, shoots, stems, pith other than *Pennisetum*.

²Rodman & Cant (1984).

³Hunt (1989), based on 1128 feeding records.

⁴Hunt (1989), based on 3891 feeding records.

⁵*Cercopithecus ascanius*; Struhsaker (1978).

⁶Mostly flowers (14.9%).

⁷*Cercopithecus mitis*; Struhsaker (1978).

⁸Mostly flowers (12.5%).

⁹*Lophocebus albigena*; Struhsaker (1978).

¹⁰Mostly flowers (5.9%).

Table 8 Significant evolutionary events.

	Ma (millions of years ago)
Divergence of chimpanzees and bonobos	2.4 ¹
Macaques in Asia	2.5 ²
Macaques quite modern in morphology, still confined to Africa, Europe	5 ³
Open habitat adapted <i>Theropithecus</i> across Africa	5 ⁴
Further acceleration of 14 Ma cooling trend	5.4 ⁵
Rapid evolution of stress-response genes in chimpanzees	<6 ⁶
Divergence of hominins and panins	6.0 ¹
Evolution of knuckle-walking	~3–8 ⁸
First papionins	6 ⁷
Increasing aridity, decreasing tree cover	6.5 ⁵
C4 grasses expand	~8.0 ⁵
Divergence of gorilla and hominins/panins	8.1 ¹
Beginning of rapid decrease in ape species numbers	8.5 ⁹
Divergence of macaques and baboons	9.8 ¹
Divergence of African and Asian colobines	10.9 ¹
Divergence of macaque/baboon lineage from other monkeys	11.6 ¹
Sharp cooling trend from climatic optimum 24–14 Ma	14.0 ⁵
Divergence of orangutans from African apes	14.0 ¹
First appearance of first well-preserved early monkey, <i>Victoriapithecus</i>	15.0 ¹¹
Divergence of colobines and cercopithecines	16.2 ¹
Divergence of hylobatids from great apes	16.8 ¹
First monkey, <i>Prohylobates</i> , likely in same clade as <i>Victoriapithecus</i>	19.0 ¹¹
Earliest monkeys, fragmentary specimens from Napak V	19.0 ¹¹
First large-bodied apes (63.4 kg female mass; <i>Proconsul major</i>)	~20.0 ¹⁰
All apes post-cranially resemble monkeys, particularly <i>Alouatta</i>	20.0
Ape, monkey teeth both adapted to ripe-fruit diet	20.0 ¹¹
Divergence of apes and Old World monkeys	23.0 ¹

¹Raaijmakers et al. (2005).²Barry et al., (1986).³Fleagle (2013).⁴Jablonski (1992).⁵Zachos et al. (2001) and Bonnefille (2010); the timing was different in different areas of Africa (Bonnefille, 2010).⁶Chimpanzee Sequencing Consortium (2005).⁷Frost & Delson (2002).⁸Kivell et al., 2009.⁹Harrison (2010a,b).¹⁰Boschetto et al. (1992).¹¹Benefit (1999).

most important niche differentiation between early apes and monkeys, affording apes the ability to displace monkeys at the most desirable feeding thus partly compensating for ape antifeedant intolerance. When extant monkeys and

apes compete directly by feeding at the same time in the same trees this contrast is critical (Houle et al. 2006). While apes may displace monkeys, smaller body size allows monkeys to feed efficiently in lower density and smaller patches. Larger body mass confers further advantages on apes; larger animals have lower per kg dietary needs and can subsist on low-quality food items such as leaves and piths (Clutton-Brock & Harvey, 1977a,b; Sailer et al. 1983); larger animals have slower gut passage, rates in larger primates can depend on microflora to process plant structural materials (Bell, 1971; Jarman, 1974; Geist, 1974; Clutton-Brock & Harvey, 1977a,b; Gaulin & Konner, 1977; Gaulin, 1979; Wheatley, 1982; Sailer et al. 1983); larger body sizes decrease terrestrial travel costs, necessary due to the dispersed nature of ripe fruits; and larger body masses lower the cost of storing energy as fat (Wheatley, 1982).

Miocene apes

Andrews (1981) noted that in the early Miocene, approximately 20 million years ago, ape species were abundant and monkey species numbers were low whereas the reverse is true for extant species. He hypothesized that monkeys established their superior antifeedant-tolerant adaptation in the Middle Miocene, and by virtue of this advantage out-competed ape species and drove down their numbers. This negative correlation has been questioned recently with updated fossil species numbers that suggest the trends are not as stark as Andrews depicted (Harrison, 2010b). Figure 15 presents Harrison's data with two differences: (i) fossil species abundance is presented as a percentage of all species described rather than raw species numbers; and (ii) extant species numbers are added (from Table 1). With these recalculations a trend similar to that of Andrews can be observed, with the exception that there is a brief resurgence of apes at about 8.5 Ma. Particularly notable is a sharp drop-off in ape species numbers after 8.5 Ma. Assuming this trend indicates a period of intense competition and great selection pressures, more rapid evolution might be expected. Shortly after the surge in monkey numbers, gorillas diverge from the panin/hominin lineage (Table 8).

The root of the ape taxon is most often considered to be found among the early Miocene (> 20 Ma) proconsuloids (Andrews, 1985, 1992; Harrison, 2010a). While some undiscovered species may yet prove to be the true ancestor of apes, proconsuloids are a stem catarrhine very close to the divergence of apes and monkeys and are therefore likely similar in morphology to the earliest apes, even if not directly ancestral (Harrison, 1982, 1987). The taxon is well represented in the fossil record and has been the subject of extensive analyses (Le Gros Clark & Leakey, 1951; Napier & Davis, 1959; Harrison, 1982, 1987; Rose, 1983, 1993, 1996; Walker & Pickford, 1983; Walker et al. 1983, 1985; Walker & Teaford, 1988, 1989; Ward, 1993; Gebo et al. 2009). While dentally quite ape-like (*ibid*; Kay, 1977; McHenry et al.,

1976), post-cranially, *Proconsul* most resembled the New World species *Alouatta* (Rose, 1983, 1993, 1996). While the genus exhibits many monkey-like characters, it also evinces a number of nascent ape-like features, to be discussed below. The early Miocene habitat has been reconstructed from analysis of a single paleosol from Rusinga preserving diverse and abundant fossils, including tree leaves (Michel et al. 2014). Multi-proxy reconstruction of the paleohabitat indicates a dense multistoried closed canopy tropical forest (Michel et al. 2014).

Three species of *Proconsul*, *P. africanus* (or *heseloni*), *P. nyanzae* and *P. major* (~20 Ma), are most often parsed from the numerous fossil individuals. Whereas *Proconsul* spp. had quite diverse body masses, they were much less diverse morphologically. Interlimb proportions were monkey-like (IMI = 96.4; Rose, 1993) and limb length itself was cercopithecoid-like (Rose, 1993). Manual phalanges were short and resembled those of cercopithecoids (Walker et al. 1983; Ward, 1993; Rose, 1993). Fragmentary ribs and humeral torsion indicate the thorax was narrow, as does the preserved narrow iliac blade (Ward, 1993). The lumbar spine had six (or possibly seven) vertebrae; vertebral morphology was monkey-like, with tall, narrow, wedged vertebral bodies and transverse processes originating from the vertebral body rather than the pedicle (Ward, 1993). The sacrum was monkey-like in morphology, but narrower (an ape-like trait; Rose, 1993), perhaps as a response to their larger body masses (Tables 2 and 9). The scapula most resembles colobines or platyrrhines (Rose, 1993), suggesting limited shoulder mobility (MacLatchy & Bossert, 1996) and an adaptation to parasagittal movement common in highly evolved quadrupeds. The humeral shaft is retroflexed, again a monkey-like trait (Fig. 2; Rose, 1993), although the function of the feature is not well understood. The distal articular surface of the humerus has a posteriorly oriented medial epicondyle, a monkey-like feature that may indicate leaping or running. Together these features suggest a less highly specialized but still monkey-like locomotor regime, adapted to walking, running and leaping.

In contrast to these monkey-like features, the trochlea and complementary articular surfaces of the ulna are more ape-like, suggesting the need for elbow stabilization which in turn suggests movement among compliant, erratically oriented terminal branches. In contrast to this ape-like morphology, *Proconsul* has a proximally extended and therefore monkey-like ulnar olecranon process that would have prevented full extension of the elbow, precluding ape-like suspensory behavior (Rose, 1993) and indicating instead the capacity for powerful elbow extension as is required for running and leaping. The capitulum is more spherical than that of a monkey, and the radial head is rather round, suggesting some rotatory capacity in the wrist (Rose, 1993); in contrast there is articulation between the ulna styloid process and carpus, limiting pronation/supination and other mobility. The olecranon fossa is oriented somewhat proximally,

a monkey-like feature (Rose, 1993). Short fingers imply that it engaged in little or no suspensory behavior.

Proconsuloids possess large, globular femoral heads and ape-like acetabula, suggesting more mobility in the hip than typical of monkeys (MacLatchy & Bossert, 1996). *Alouatta*, which *Proconsul* resembles, feeds in a hindlimb suspensory posture, though also using a prehensile tail in conjunction with the hindlimbs; the mobile *proconsuloid* hip suggests a similar strategy, albeit without the tail. However, in addition to a globular femoral head, the greater trochanter is expanded cranially (Fig. 14; Rose, 1993: fig. 12.7), a monkey-like feature that increases power during leaps; the long *Proconsul* ischium is also a leaping adaptation (Rose, 1993). As is the case with New World monkeys, *Proconsul* lacked monkey-like ischial sitting pads, often interpreted as a sleep-sitting adaptation (Washburn, 1957). The breadth of the distal femoral articular surface is broader than in monkeys (Rose, 1993) but is not fully ape-like; this may be an allometric consequence of large body mass. The shaft and distal articular surface of the tibia is more ape-like than monkey-like (Rose, 1993), suggesting ape-like ankle mobility rather than a more hinge-like joint of monkeys. The lateral rays of the foot are monkey-like, suggesting a leaping adaptation, but there is a robust great toe that indicates a more ape-like than monkey-like vertical climbing capacity.

The teeth of *Proconsul* suggest a 'superfrugivore' (Kay, 1977) and a dependence on ripe fruit. There is no morphological indication that piths and herbaceous items were important to the *Proconsul* diet; THVs were presumably added only when apes adapted secondarily to terrestrial travel, thus encountering terrestrial food items more often. Dental morphology suggests early apes had a ripe-fruit diet, but the lack of suspensory adaptations indicates that they collected fruits in the central core of the tree canopy rather than the terminal branches.

Taken together these characters suggest a primate that is better adapted than monkeys to foraging among the erratically placed, small-diameter, compliant branches in the tree edges, perhaps engaging in more hindlimb suspension than is seen in extant apes. Movement among such unstable supports requires powerful stabilization of the limbs to counter unstable support and relatively slow, careful movement rather than a monkey-like walking and running punctuated by spectacular leaps. Leaping adaptations, even if less highly evolved than in extant monkeys, suggest a feed-as-you-go, leap-between-trees foraging regime, much like that of monkeys, but more like that of ceboids such as *Alouatta* or *Cebus* than African arboreal monkeys.

If early dates of 20.6 Ma for *Morotopithecus* are correct, apes evolved some quite advanced features, such as broad thoraxes, long forelimbs and long, curved manual phalanges (MacLatchy et al. 2000). Others prefer dates of 15 Ma or even later (Pickford et al. 1999) for this fossil. Suspensory morphology suggests to the author that the later dates

Table 9 Hypotheses or research foci worthy of further investigation.

Hypothesis or issue	Sources
Wide interorbital distances are an adaptation to leaping, improving depth perception	Hunt & Borniger, <i>in prep</i>
Food resource distribution is dispersed for montane and desert baboons and chimpanzees, yielding weakened female bonds in each	Wrangham (1977, 1979, 1980); Jolly (2001); Byrne et al. (1990)
A posteriorly reflected medial epicondyle increases the moment arm of the digital flexors during 'toe' off as an adaptation to running and leaping	This study, Fig. 4
The monkey vertebral ventral keel resists stresses on the ventral edge of lumbar vertebrae generated during lumbar extension during leaping and running	This study
The keel functions as the attachment site for the anterior longitudinal ligament; it increases the moment arm the ligament applies to prevent hyperextension of the column during leaping and running	Sarmiento, <i>pers. comm.</i>
The humeral flared medial trochlear margin or keel resists moments normal to the keel surface generated by elbow extensors and digital flexors during elbow extension	Jolly (1972); Jenkins (1973); this study, Fig. 5
Which monkeys engage in hand over hand vertical climbing on vertical or near-vertical supports?	This study, Table 3
Large supraorbital tori are an adaptation that reduces the risk of eye injury during agonistic encounters	Tappen (1973); this study
Cheek flanges reduce the risk eye injury during agonistic encounters	This study
For trees utilized by both chimpanzees and monkeys, monkeys feed in the tree earlier in the fruiting cycle and chimpanzees later; simultaneous feeding is rare	Wrangham (1980); Wrangham et al. (1998); this study
Monkeys preferentially deplete fruits in the tree core, leaving a dis-proportionate number of fruits in the tree periphery	This study
For trees utilized by both chimpanzees and monkeys, chimpanzees feed closer to the tree periphery and among smaller diameter branches	Avis (1962); Wrangham (1980); Hunt (1992a); this study
Monkeys avoid the tree periphery to avoid raptors, not due to the difficulty of negotiating small, compliant supports	Sarmiento, <i>pers. comm.</i>
Monkeys and apes feed equally often in the tree periphery and among smaller diameter branches	Houle et al. (2006, 2007, 2010, 2014)
Large body size among apes evolved in parallel with monkey bilophodonty as a response to monkey/ape competition	This study
Full forelimb abduction occurs during vertical climbing and evolved as an adaptation to high frequencies of vertical climbing and/or the importance of vertical climbing in accessing vital resources	Fleagle et al. (1981); Isler (2005)
Unimanual suspensory behavior (arm-hanging) is not an important and/or frequent behavior among chimpanzees, compared to monkeys	Doran (1993)
Unimanual suspensory behavior (arm-hanging) is an important and frequent behavior among chimpanzees, compared to monkeys	Hunt (1992a)
A reduced olecranon process and the capacity to completely extend the elbow is an adaptation to vertical climbing, not suspensory behavior	Fleagle et al. (1981); Doran (1993); Isler (2005)
A reduced olecranon process and the capacity to completely extend the elbow is an adaptation to arm-hanging, less an adaptation to climbing	Rose (1983, 1988b, 1993); Hunt (1992a); this study
Long forelimbs are adaptations to vertical climbing with less selective pressure exerted by armhanging/terminal branch foraging	Fleagle et al. (1981); Cartmill (1974); Jungers (1976)
Long arms are an adaptation to suspensory feeding and terminal branch positional modes but less or no adaptation to vertical climbing	Tuttle (1969); Grand (1972)
Long arms are an adaptation to both vertical climbing and armhanging	Sarmiento (1985 et seq.); Fleagle (2013); Hunt (1991)
Short hindlimbs among apes are evolved to lower the center of gravity when locomoting on compliant supports	Jungers (1984)
Chimpanzees have palm-walking morphology adapted to provide stability and support when the hand is dorsiflexed and the wrist supinated with palm contacting the substrate	This study
Chimpanzees ignore some otherwise appealing fruit-bearing trees when no 3–10 cm diameter vertical supports are available, raising climbing costs	This study
Ischial callosities are a sleeping adaptation; ischial callosities are found sporadically among chimpanzees suggesting late evolution of sleeping platforms	Washburn (1957); this study

Table 9 (continued)

Hypothesis or issue	Sources
The small hallux of orangutans is attributable to a unique heel-against-toes grip during vertical climbing	Sarmiento (2012)
The selective advantage of knuckling hand positioning is to reduce moments on the manus and perhaps carpus during knuckle walking/running	Tuttle (1969, 1970)
A steeply angled zona conoidea and beveled radial head prevent medial dislocation of radial head during 'dynamic' armhanging (hang-feeding)	This study
Large, ventrally extended coronoid process functions to increase the moment arm for <i>brachialis</i> to initiate elbow flexion during armhanging	This study
Arm-raising or forelimb abduction is accomplished partly by a scapular-clavicular lever powered by serratus anterior; sternoclavicular articulation is the hinge; trapezius contributes little to arm-raising	Oxnard (1963, 1967); Larson et al. (1991); Larson (2015); this study
A cranial set to the shoulder, i.e. tilted up glenoid fossa, reduces tensile stresses on the caudal (inferior) fibers of the glenohumeral joint capsule and allows cranial fibers to bear some weight during unimanual suspension	Hunt (1991)
A broad sternum reduces bending stresses on the clavicle	This study
A cone-shaped thorax is an adaptation to arm-hanging and reduces compressive stresses on the ribcage	Hunt (1991)
The larger surface area of ilium in great apes is an allometric phenomenon evolved to retain mechanical equivalency for hip extension in heavier species	Stern (1971)
The ape narrow sacrum evolved to allow larger hip extensor attachment areas on the ilia; N.B. siamang v gibbon	This study
A long os coxa and long isthmus reduce bending moments on the lumbar vertebrae during vertical climbing, particularly during ipsilateral support	This study
Hylobatid iliac breadths, sacral breadths, lumbar vertebral numbers, os coxa length and cone-shapedness of the thorax form an allometric series	This study
Broad knees among apes are an allometric response to greater bending bending moments on the knee during one-limb stances; greater stresses are generated due to broad thoraxes and pelvis among apes	This study
The common ancestor African apes and human had a gorilla- or hamadryas-like social	Swedell et al. (2012); Crompton, this volume; this study
The common African ape/human ancestor resembled gorillas	Multiple sources; see text
Male patrolling and high levels of coalitionary killing among chimpanzees evolved after the chimpanzee-human split	This study
Rapidly evolving genes in chimpanzees are related to the recent evolution of male bonding, male territoriality and coalitionary killing	This study

are more likely, noting that the discoverers are quite confident in the early date.

Early Miocene monkeys

The earliest known monkey, *Prohylobates*, dates to approximately 18 Ma, perhaps 3 Ma prior to the divergence of colobines and cercopithecines (Table 8; Benefit, 1999), but 3 Ma after the divergence of apes and monkeys (Table 8); little is known of its post-crania, but the dentition is well-studied. Molars are not bilophodont, but instead possess a crista obliqua that fills what would be the trough that separates the mesial and distal trophs in extant Old World monkeys to form the characteristic monkey bilophodont morphology (Benefit, 1999). Details of cusp height, cusp arrangement and the shape of the shearing crests suggest a diet dominated by fruits, which are estimated as constituting 79% of the diet (Benefit, 1999), a dramatically higher

proportion of fruit than seen in extant monkeys and greater even than that for apes. The rather ape-like molar morphology of early monkeys suggests that their diet was not just any fruits, but fruits that were structurally similar to those apes eat, ripe fruits. For example, Andrews & Martin (1991) noted that 'the dietary category of ancestral catarrhines and earliest hominoids is widely interpreted as soft-fruit frugivory' (p. 206); soft fruits are ripe fruits, which indicates a dietary regime resembling that of extant apes, not extant monkeys. Extant monkey dentition, with its high, bilophodont cusp morphology, larger surface area and longer shearing crests is adapted to comminuting tough food items finely, even down to the level, perhaps, of individual cells, increasing the digestibility of cellulose and complex carbohydrates (Walker & Murray, 1975; Sheine & Kay, 1977; Kay, 1978; Kay & Hylander, 1978; Kay & Sheine, 1979; Sheine, 1979, 1982; Temerin & Cant, 1983). These are adaptations to digesting unripe fruit and foliage.

While there are fewer post-cranial fossils of proto-monkeys than early apes, the post-crania *Victoriapithecus* are abundant enough to show that this species falls within the range of variation in extant cercopithecoids (Harrison, 1989; McCrossin & Benefit, 1992; Benefit, 1999), perhaps resembling most the semi-terrestrial vervet, *Chlorocebus aethiops* (Harrison, 1989; McCrossin & Benefit, 1992). The proximal humerus is retroflexed, the olecranon process is long, phalanges are short and monkey-like, great toe abduction is limited compared with that of apes, the greater tubercle extends above the humeral head and the acetabulum is small, consistent with the limited femoral joint excursion seen in monkeys rather than apes (Harrison, 1989; Benefit, 1999). The ischium is long, indicating a long lever arm and large PCSA for hip extensors, an adaptation to leaping, climbing and quadrupedalism. Ischial morphology indicates the presence of ischial callosities. *Victoriapithecus* had a tail.

In summary, in the early Miocene the substantial neontological niche separation between apes and monkeys had only just begun to evolve, and monkeys and apes differed little post-cranially, cranially or dentally. Since then apes have evolved quite different bodies but their dentition has remained relatively unchanged, suggesting that ape diets are little changed from their earliest appearance (Pilbeam, 1996, 2002); monkeys in contrast have kept their early Miocene body plan but evolved bilophodont dentition. Monkeys have evolved to eat ever less ripe fruit and as they refined their unripe fruit adaptation their species numbers and population density increased, particularly after 8.5 Ma. While monkeys eat different foods than in the early Miocene, they gather it in a manner that has changed little in 20 Ma. Extant apes find that by the time fruit is edible to them as many as 10 species of monkeys have already depleted the fruit crop in the tree core, utilizing their ancient sit-to-feed adaptation. What remains is a hollow sphere with ripe fruit in the peripheral compliant, small-diameter branches where non-stereotyped postures and arm-hanging are required to feed (Fig. 16). For chimpanzees, the sparse and dispersed nature of these leftovers requires terrestrial travel between food sources and vertical climbing to reascend trees. Inevitably, the large number of monkeys depleting the fruit crop leaves some individual trees so overharvested that what little fruit is left is not worth gathering, leaving their food supply even sparser and more dispersed.

Middle and late Miocene apes

Morotopithecus (MacLatchy et al. 2000) has been reconstructed with a broad thorax and quite chimpanzee-like scapula. Other ape features such as lumbar reduction occur later in the Miocene, ~12 Ma (Moyá-Solá et al. 2004; Ward, 2007; Russo & Shapiro, 2011; Ivette et al. 2014; for review, see Crompton et al. 2008). *Dryopithecus* (10–12 Ma), a closed-canopy adapted primate, strongly resembles extant

chimpanzees in molar and premolar dimension and enamel thickness (Alba et al. 2010), gracile zygomatics, long, curved phalanges and possibly a chimpanzee-like IMI (Kordos & Begun, 1997; Begun, 2010; Begun et al. 2012), but a close phylogenetic relationship to panins is often deemed unlikely (Crompton et al. 2008; Harrison, 2010a,b).

While it is not clear which ape from later in the Miocene is ancestral to the panins, consistency in dental and facial morphology among the various candidates leaves the craniodental morphology less in doubt. As the Miocene progresses there is a tendency toward more robust faces and larger, more thickly enamelled premolars and molars; *Nakalipithecus* (Kunimatsu et al. 2007), *Pierolapithecus* (Alba et al. 2010), *Samburupithecus* (Ishida & Pickford, 1997), *Ouranopithecus* (Koufos & de Bonis, 2005) and *Anoiapithecus* (Alba et al. 2010) had large thick-enamelled molars and small canines. Where mandibles exist, they are robust. While each of these taxa could be described as more gorilla-like than chimpanzee-like, *Chororapithecus* (10 Ma; Suwa et al. 2007) shows very strong affinities to gorillas. It seems most likely that thick postcanine dental enamel is primitive for the great ape and human clade (Andrews & Martin, 1991; Alba et al. 2010).

Reduced canine dimensions have implications for the reconstruction of late Miocene ape social behavior, suggesting that the level of interindividual violence observed in panins evolved after 9 Ma. While some have speculated that there may be a negative correlation between canine and cheek tooth dimensions, driven largely by gape limitations arising from increased mandibular ascending ramus height, Plavcan & Daegling (2006) demonstrated that cheek tooth size and canine size are unrelated.

The robust-faced *Ouranopithecus macedoniensis* (9.6 Ma), often cited as a common ancestor of humans, chimpanzees and gorillas (de Bonis & Koufos, 1994; Koufos & de Bonis, 2005), has a body mass somewhat greater than that of chimpanzees, estimated at 72 kg (160 lbs) for males, with females perhaps half that. The *Ouranopithecus* face resembles that of gorillas but has a low zygomatic origin and tall squared-off, robust zygomatics, reminiscent of australopiths. *Ouranopithecus* molars and premolars are larger than those of gorillas, despite their smaller body mass; cusps cluster toward the center of the tooth, a feature found in the teeth of *Au. africanus*; incisors are large and thus great ape-like (*ibid*; Güleç et al. 2007). Females have such dramatically reduced canines that they are diamond shaped in profile and do not extend above the tooth row (*ibid*).

Ouranopithecus post-crania are poorly known, but two well-preserved phalanges are shorter than would be expected for a chimpanzee (given body size differences) and resemble those of terrestrial quadrupeds (de Bonis & Koufos, 2014). They are ventrally curved, approaching the curvature seen in chimpanzees. Small flexor sheath ridges are apparent (de Bonis & Koufos, 2014). If this species is indeed the common ancestor of *Pan*, *Gorilla* and hominins,

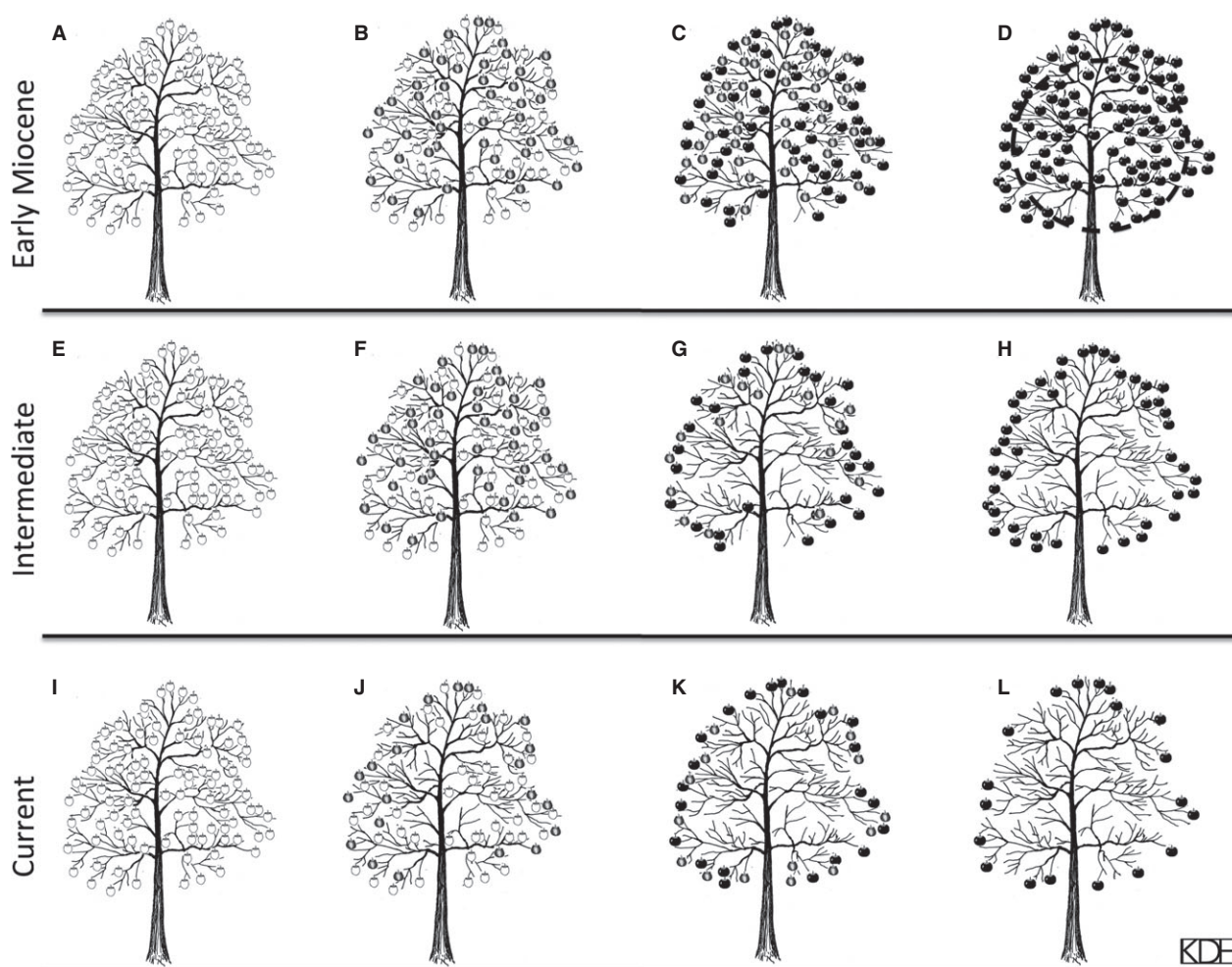


Fig. 16 Hypothetical change in ripe fruit resources available to apes from the early Miocene (A–D) to the present (I–L). In the early Miocene both the recency of the divergence of cercopithecoids and hominoids, dental morphology and the similarity of ape and monkey dentition suggest that both lineages were adapted to a ripe fruit diet. A fruiting tree was unlikely to have been visited by primates when fruit was first set and completely unripe (A), and likewise during times of moderate fruit abundance a fruiting tree might have few or no fruits taken when its fruits were unripe or partly ripe (B). During an abundant season even a tree with ripe and partly ripe fruit might remain undepleted (C), and only when fruits were completely ripe would monkeys and apes harvest it (D). The morphology of *Proconsul* suggests some nascent adaptation to terminal-branch feeding. Thus, proto-apes and proto-monkeys might occupy different harvesting niches, with proto-monkeys harvesting from the tree core (D: inside dotted line) while proto-apes might be compelled to gather some percentage of their food in the tree periphery (outside the dotted line). As monkeys harvested fruits earlier and earlier in the fruiting cycle, remaining fruits formed more of a hollow sphere, forcing apes into the compliant terminal branches (H). Currently as many as 10 species of monkey harvest unripe fruit and partly ripe fruit (J) still earlier in the fruiting cycle, separating their harvesting time further from apes and leaving not only a hollow sphere (K, L), but given the sheer number and variety of monkey species little fruit is left for apes (L). At some tipping point ripe fruit became so sparse (L) that a threshold was reached where traveling arboreally was inefficient because it required traversing numerous tree crowns at which point descension, traveling terrestrially and reascending evolved.

knuckle-walking and fully evolved arm-hanging evolved after the divergence.

The robust but otherwise gorilla-like morphology of *Ouranopithecus* articulates with growing neontological evidence suggesting that the last common ancestor of gorillas, chimpanzees and humans was gorilla-like. A reconstruction of African ape life-histories concludes the gorilla condition is primitive (Duda & Zrzavy, 2013). The last common ancestor of African apes and humans has been argued to be gorilla-like in thumb morphology

(Almécija et al. 2015), hand/forelimb proportions (Schultz, 1930), foot morphology (Schultz, 1930, 1950; Crompton, this volume), foot static loading (Wang & Crompton, 2004), ecology (Crompton, this volume), climbing behavior (*ibid*), bipedalism (*ibid*) and kinematics of load carrying (Watson et al. 2009). Furthermore, features shared among Miocene apes and early hominins such as great sexual dimorphism (Kelley, 1995a,b) and scapular morphology (Alemseged et al. 2006) suggest gorilla-like features persisted in the *Pan*/hominin lineage for some time

after gorillas branched off. Some have suggested a gorilla-like or hamadryas social system was the primitive African ape social structure (Swedell & Plummer, 2012); hamadryas baboons share with gorillas a polygynous social structure where unrelated females are bonded to a single breeding male.

Evidence for parallel evolution among the great apes

Because orangutans are the most superbly arboreally adapted great ape, they are the strongest argument for the parallel evolution of 'brachiating' characters. *Sivapithecus* (8–13 Ma) is widely considered either a direct ancestor of orangutans or close to the ancestral lineage of extant orangutans, yet the 12.3 Ma *Sivapithecus* has a narrow pelvis and therefore probably a narrow, monkey-like thorax (Morgan et al. 2015). The *Sivapithecus* humerus is monkey-like in that it has a flat deltoid plane, prominent deltopectoral and deltotriceps crests, mediolateral curvature and proximal humeral retroflexion. It has a somewhat ape-like distal articular surface, with a quasi-spool-shaped trochlea (Rose, 1989; Pilbeam et al. 1990); carpals and a fragmentary radius are largely *Proconsul* or monkey-like in suggesting little wrist flexibility (Rose, 1993). Femoral fragments, a navicular and several phalanges are interpreted as consistent with vertical climbing but not suspensory behavior (Madar et al. 2002). As with *Proconsul*, there is some indication of hip mobility (Rose, 1993). These details suggest a rather monkey-like, semi-terrestrial positional repertoire with vertical climbing and (given hip mobility) present but low levels of suspensory behavior on the order of that reconstructed for *Proconsul*.

Whichever the ancestor of the panins is, suspensory behavior evolved independently in orangutans and African apes. If *Dryopithecus* is in the lineage of extant African apes, the presence of 'brachiating characters' in that lineage means such features evolved quite early and independently of Asian apes. If instead *Ouranopithecus* or some related species is the African ape and human common ancestor, then African apes and orangutans evolved suspensory behavior not only independently, but quite late in their evolutionary history. A further parallelism after the split of Asian apes might be quadrupedal knuckle-walking; Dainton & Macho (1999), Inouye & Shea (2004) and Kivell et al. (2009) offer compelling evidence that quadrupedal knuckle-walking evolved independently in gorillas and chimpanzees. These authors show that most features hypothesized to be adaptations to knuckle-walking (beaked scaphoid, dorsal concavity of the scaphoid, waisting of the capitate, distal concavities on the hamate and capitate, dorsal ridges on the hamate and capitate) are much more variable among the African apes than previously appreciated, and those that are consistent appear at different developmental stages among the knuckle-walking apes (Kivell et al. 2009), suggesting independent

origin. The authors conclude that knuckle-walking appeared independently in gorillas on the one hand and the ancestor of chimpanzees and bonobos on the other. Paleontological evidence (Corruccini & McHenry, 2001; *contra* Richmond & Strait, 2000) suggests that hominins did not have a knuckle-walking ancestry. That they did not would reinforce evidence that the constellation of anatomical, physiological and social traits that characterize chimpanzees and gorillas evolved relatively recently. Rose (1993, 1996) argues that suspensory behavior evolved independently in several further lineages unrelated to extant apes, including the gibbon-sized ~11 Ma Miocene catarrhine *Pliopithecus*, several small Miocene apes, hylobatids, *Dryopithecus*, *Oreopithecus* (7–9 Ma), orangutans and African apes. Suspensory atelines must be added to this list (Larson, 1998). As unlikely as such massive parallelism might seem, Larson (1998) has documented 35 characters (a subset of those in Table 4) that she argues have evolved independently in the New World atelines (see also Fig. 13) and apes, suggesting that suspensory characters are an often-evolved solution to primate ecological challenges. Yet another lineage, the odd-nosed monkeys, has also evolved these suspensory features independently (Covert et al. 2006; Su & Jablonski, 2009).

The ubiquity of the homoplastic evolution of morphology linked to suspensory behavior suggests that these ape features evolved in response to a similar, novel selective pressure – the steady increase in monkey population numbers (Andrews, 1981; Temerin & Cant, 1983). Independently, each of the apes and other now-extinct suspensory primates faced a dwindling food supply that was found ever-farther from large branches in the tree core, demanding the collection of food items using suspensory behavior. The chimpanzee lineage in particular encountered several selection pressures in a relatively short period of time (Table 8). The first baboons, which would compete with chimpanzees in any terrestrial activity, may have emerged as early as 9.8 Ma when macaques and baboons diverged (Raaum et al. 2005), although the earliest appearance of fossils representing terrestrial papionins (*Theropithecus oswaldi*) only appear at 5 Ma (Eck, 1993). There is evidence of a dramatic decrease in tree cover at 6.5 Ma (Bonnefille, 2010), and at 5.4 Ma there was a rapid cooling event that is thought to have again decreased tree cover. By 5 Ma the dry habitat adapted *Theropithecus* was ubiquitous across Africa (Table 8).

Evidence for rapid evolution in the Panini: genetics and species counts

The ~9 Ma inflection in ape and monkey species numbers (Harrison, 2010b) and evidence that specializations characterizing extant apes appeared at the same time, and in parallel in the various ape lineages, suggests a relatively rapid rate of evolution among apes from the late Miocene to the

present. Human and chimpanzee genomic data are consistent with this scenario. It might be expected that even if features shared in common among the apes are late-evolving parallelisms, dramatic changes in the hominin lineage including brain expansion, loss of body hair, muscle mass reduction (particularly in the masticatory apparatus), anatomy related to speech acquisition and anatomy related to upright walking are unassailable evidence that humans have evolved more rapidly than apes. This in turn might suggest that humans should bear more positively selected genes than chimpanzees, but this is not the case; chimpanzees have more positively selected genes than humans (Bakewell et al. 2007) and thus have changed more genetically since the ape/human divergence than humans. While the difference is not large, 233 genes positively selected for chimpanzees vs. 154 for humans (Bakewell et al. 2007), the trend is the opposite of what most specialists would have predicted.

The function of many genes that have evolved rapidly among chimpanzees is poorly understood at present, genes for protein metabolism, mRNA transcription, nucleic acid binding, nuclease function, transferase function (Bakewell et al. 2007) for example, but those for which function is known offer surprising confirmation of the fossil evidence for ape evolution. Among chimpanzees, genes associated with stress response have evolved rapidly: there are 14 positively selected genes in chimpanzees vs. two in humans (Bakewell et al. 2007). Sixteen genes controlling proteolysis have been positively selected among chimpanzees vs. only two for humans; proteolysis is involved in wound healing. The chimpanzee Y chromosome has undergone rapid evolution since humans and chimpanzees diverged, losing large segments of the MSY protein-coding regions, numerous other gene families and at the same time acquiring twice as many massive palindromes as humans, a divergence characterized as 'extraordinary' (Hughes et al. 2010). Chimpanzees have lost three genes that regulate inflammatory response, *IL1F7*, *IL1F8* and *ICEBERG* (Bakewell et al. 2007), genes still found in humans, gorillas and orangutans (Chimpanzee Sequencing Consortium, 2005). The loss is hypothesized to reduce the risk of sepsis (Mikkelsen et al. 2005), suggesting an increase in wounding and infection in chimpanzees since the human/chimpanzee split. Genetic evidence for increased violence and aggression in the chimpanzee lineage is in accord with the increase in canine dimensions since the Miocene (see above).

After the chimpanzee/human split, chimpanzees also lost genes *APOL1* and *APOL4* (Chimpanzee Sequencing Consortium, 2005); *APOL1* has been proposed to be a lytic factor that provides some resistance to sleeping sickness, a disease caused by the parasite *Trypanosoma brucei* (Vanhamme et al. 2003). The vector for sleeping sickness is the tsetse fly (*Glossina* spp.), which largely limits its activities to within 3 m of the forest floor (Buxton, 1955; Omooguna, 1985). The

presence of *APOL1* in humans and its loss in chimpanzees suggests that chimpanzees became more arboreal after the divergence of the two lineages, because arboreal activity and particularly arboreal sleeping would remove them from the range of the *Trypanosoma* vector, allowing a mutation in the gene to fixate. The common ancestor of chimpanzees and humans likely slept terrestrially, as do most gorillas. This supports evidence that a large bodied ape such as *Ouranopithecus* was the common ancestor, assuming that a large ape might sleep terrestrially, as gorillas do.

Taken as a whole, genetic evidence suggests that chimpanzees have acquired an enhanced capacity to cope with stress and injury in the past 6 Ma. This in turn suggests that the violent, male-bonded territorial aspects characteristic of extant chimpanzees evolved some time after humans and panins diverged.

Evidence that *Proconsul* was a 'superfrugivore' and evidence for a relative lack of monkey competitors suggest that compared with extant chimpanzees, proconsuloids experienced the forest as richer. Concentrated arboreal resources are defensible and defensible resource distribution among extant primates elicits a female-bonded social system (Wrangham, 1980). Such a system contrasts markedly to that of extant apes, none of which have close bonds among female kin (Sterck et al. 1997; Wrangham, 1979). At some unknown point in the MioPliocene, hypothetically in response to competition from an expanding population of monkeys, the ape foraging strategy changed, making female resource defense impossible, and ultimately yielding in the current variety of ape social systems.

A shift away from female-bonding in the face of changes in resources is not merely theoretical. As discussed above, terrestrial cercopithecines in unproductive environments such as deserts and montane habitats have also lost female bonding (Byrne et al. 1990; Jolly, 2001). When female bonding is lacking, social structures may take diverse forms. While the vast majority of monkeys have similar social systems, ape social systems are extraordinarily varied, possibly strongly influenced by travel costs (Wrangham & Rubenstein, 1986). Orangutans and gibbons are almost completely arboreal (Rodman & Cant, 1984; Cannon & Leighton, 1994), imposing higher travel costs compared with terrestrial species. Restricted diets and/or high travel costs limit group size and result in the 'solitary'/fission-fusion and monogamous systems of Asian apes. Uniformly high levels of body mass dimorphism in *Ouranopithecus*, gorillas, orangutans and australopithecines (McHenry, 1986), in contrast to monogamous hylobatids and to chimpanzees, suggest that the common ancestor of humans and chimpanzees may have had a more gorilla-like social system, or a multilevel variation of the gorilla system (Swedell & Plummer, 2012), rather than a chimpanzee or bonobo system. If this scenario is correct, as African ape ancestors experienced food resources as scarcer and more dispersed gorilla social groups became smaller and single male, and chimpanzees evolved a more fission-

fusion society with the accompanying imbalances of power that selected for the extreme violence of chimpanzee society.

Conclusion

The overlap of ape and monkey food species lists, the ability of monkeys to tolerate high levels of cellulose, tannins and alkaloids, the reversal in ape and monkey species abundance, the gradual emergence of monkey bilophodonty and ape suspensory anatomy together suggest a 20 million year history of competition and co-evolution between monkeys and apes. Without this competition, evidence suggests that monkeys would not have their distinctive bilophodonty and digestive physiology and apes would not have their large body size, advanced cognition and anatomical specializations. There is strong support for the hypothesis that ape anatomy evolved to accommodate positional behaviors (arm-hanging, suspensory locomotion) that are adaptations to harvesting fruits and occasionally other items from among the compliant supports in the outermost periphery of the tree canopy. The dispersed distribution of extant ape food resources discourages large group sizes, and as a consequence ape feeding parties or social groups are small compared with monkeys. The sparse, dispersed nature of food resources has also selected for terrestrial travel in great apes, necessitating adaptations to reascending trees after travel between feeding sites.

Early Miocene proconsuloid abundance, dental adaptations to a ripe-fruit diet and post-cranial anatomy adapted to walking and leaping all suggest proto-apes possessed a monkey-like food harvesting regime, in turn suggesting that the ancestral ape social system was female-bonded. Over the last 20+ Ma apes and monkeys have diverged from a shared ancestral female-bonded, ripe-fruit, feed-as-you-go adaptation, with monkeys evolving adaptations to more antifeedant-rich diets while retaining ancestral positional adaptations, whereas apes retained a focus on ripe fruit but evolved new positional adaptations.

Evidence from genetics, paleontology and primate ecomorphology suggests that ape adaptations continued to evolve rapidly well into the Pliocene and likely are evolving still. The sharp inflection in curves for ape and monkey abundance in the late Miocene offers an approximate timing for the loss of female-bondedness among apes.

Evidence that the gorilla morphotype was the ancestral condition among African apes including evidence for large body mass, ponderous movement, terrestrial sleeping sites and great sexual dimorphism are consistent with speculation that the common ancestor of the great apes had a polygynous female-choice system similar to that of gorillas, perhaps with the addition of male bonds among breeding groups, a system similar to that of hamadryas baboons (Swedell & Plummer, 2012).

Ape-like 'brachiating morphology' (Fig. 9; Table 5) appears to have arisen independently many times and in many different lineages, including each of the ape tribes, fossil species such as *Oreopithecus*, New World atelines and odd-nosed monkeys. Circumstantial evidence suggests that the selection pressure driving the independent evolution of suspensory adaptations is competition from monkey morphs. The power of ecology and competition to drive the evolution of ape-like ecomorphology is particularly evident in convergence between New World atelines and chimpanzees. Despite approximately 40 million years of independent evolution, there is a striking convergence between the two taxa; 11 features that distinguish apes from other primates evolved independently in the atelines (Larson, 1998), and atelines share with chimpanzees not just morphology, but a territorial, male-bonded, fission-fusion, border-patrolling, coalitionary violence bearing social system (Aureli et al. 2006). This convergence suggests a powerful relationship among the distribution of food resources, food chemistry, suspensory adaptations and social system. The repeated pattern of niche differentiation leading to the evolution of suspensory behavior suggests that there is, if not an inevitability, a strong tendency for primate communities to evolve monkey/ape contrasts given geologic timescales.

There are, of course, alternative interpretations, and many of the hypotheses supporting this conclusion remain to be tested, but articulating one possible evolutionary scenario may be helpful in spurring tests of the many hypotheses and speculations bound up in it. Some fruitful areas for future research are suggested in Table 9.

Acknowledgements

The author is grateful to SKS Thorpe for inviting him to compose this article, and for numerous helpful discussions throughout its composition. Research was supported by NSF BCS-0002686 and SGER BNS 97-11124 to KDH, BNS-86-09869 to RW Wrangham, the Indiana University Foundation, the Indiana University Office of the Vice Provost for Research, the Stone Age Institute, MG Hunt and M McCourt. Conversations and email with RH Crompton, JG Fleagle, A Houle, SH Hurst, RF Kay, RW Wrangham and especially EE Sarmiento were of great benefit. Equally important were the insights and lucid writing of MD Rose, particularly his extraordinary *Another Look* article (Rose, 1988b). Comments by two anonymous reviewers improved the manuscript immensely. The many errors that still remain are, of course, the author's alone.

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